CRETACEOUS AMMONITES AND NAUTILOIDS FROM ANGOLA

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CONTENTS

SYNOPSIS

Five separate faunas are described from a collection of over 250 Cretaceous ammonites and nautiloids from Angola. They are as follows:

(1) 9 *Douvilleiceras* from Dombe Grande, which fix the age as the Mammillatum Zone, Lower Albian.

(2) About 50 *Neokentroceras* from Praia do Jombo, north-east of Lobito, which are the best specimens yet found of the genus, and are of low Upper Albian age.

(3) 85 ammonites of the genera *Anagaudryceras*, *Gaudryceras*, *Didymoceras* (including *D. subtuberculatum* sp. nov.), *Polyptychoceras*, *Kitchinites* (*K. angolaensis* sp. nov.), *Desmophyllites*, *Oiophyllites*, *Eupachydiscus*, *Hoplitoplacenticeras* and *Tetragonites* from Egito, which fix the age as the Vari Zone, Upper Campanian.

(4) 26 ammonites of the genera *Neophylloceras*, *Baculites*, *Nostoceras* (including *N. rotundum* and *N.* (?) *obtusum* spp. nov.), *Polyptychoceras*, *Manambolites* (*M. dandensis* sp. nov.) and *Sphenodiscus* from Barra do Dande, of which the *Sphenodiscus* is probably Upper Maastrichtian, while all the remainder are either Polyplocum Zone, Upper Campanian, or basal Maastrichtian.

(5) 6 *Baculites* and *Didymoceras* from Carimba, of Upper Campanian age.

The description of *Baculites subanceps* from Carimba has made necessary a full revision of the European species *B. anceps* Lamarck; the type population from Manche, France, is described, a selection of specimens are figured and a neotype is designated.

I INTRODUCTION

The bulk of the ammonites described in this paper were collected between 1928 and 1931 by Henrique O'Donnell and Alexandre Borges, both of Serviço da Carta Geologica of Angola (now superseded by the Serviços de Geologia e Minas at Luanda). O'Donnell sent 221 cephalopods (210 ammonites and 11 nautiloids) to Dr. L. F. Spath for determination and description in 1930. They are now in the collections of the British Museum (Natural History) and consist of the following:

81	ammonites from the Upper Albian of Praia do Jombo.
7	ammonites from the Cenomanian of Salinas.
1	ammonite and 2 nautiloids from the Senonian of San Nicolau.
7	ammonites (1 now lost) from the Campanian of Carimba.
10	ammonites from the Campanian of Benguela.
85	ammonites and 9 nautiloids from the Campanian of Egito.
19	ammonites from the Campanian and Maastrichtian of Barra do Dande.

Efforts were made by Spath from September 1930 to October 1935 to reach agreement with O'Donnell and later with Fernando Mouta on the cost and place of publication of a full description of this collection, but satisfactory terms could not be agreed upon. The negotiations with Mouta were reopened in 1950 with the result that Spath was then able to publish his "Preliminary notice" of the collection in 1951. Spath was never able to start on the full description he had wanted to publish for so long, and only now, 35 years after the collection first arrived here, is it possible to present the full description that the ammonites clearly deserve. Previous references to the collection as a whole were made by Mouta & O'Donnell (1933: 64) and Mouta (1938: 33). The 7 Cenomanian ammonites from Salinas were described by Spath (1931: 316), and they all belong to species described by Douvillé (1931). The Egito ammonites were also referred to by Spath (1940*a*: 52). Finally both the Egito and Barra do Dande faunas were listed and discussed by Spath (1953: 49–50) in his paper on the Antarctic Campanian cephalopod fauna, and five of the specimens were figured (Spath 1953, pl. 2, fig. 6; pl. 3, fig. 6; pl. 6, fig. 6; pl. 7, fig. 7; pl. 13, fig. 7).

Descriptions of the lamellibranchs, gastropods and echinoids collected at the same time by O'Donnell were also delayed; the lamellibranchs and gastropods were described by Rennie (1945) and the echinoids by Dartevelle (1952: 27; 1953).

Alexandre Borges was less successful in sending his ammonites to Spath for description. He had concentrated on collecting examples of *Douvilleiceras* from localities between Benguela and Dombe Grande in 1930 and 1931 and had finally obtained over 50 specimens. These he attempted to send to Spath in 1931 and again in 1932, but for some unknown reason the collection never left Angola. Through the kindness of the Director of the Servicos de Geologia e Minas at Luanda I have been able to see and describe the 9 specimens which are all that now remain of the original 50 *Douvilleiceras*.

Other collections of Angolan ammonites in the British Museum (Natural History) that are described here are the 7 heteromorph ammonites collected by Mr. Beeby Thompson at Barra do Dande in about 1915 that were referred to by Spath (1921: 56), 6 examples of *Neokentroceras* from Catumbella purchased from Dr. W. J. Ansorge in 1905, and the *Neokentroceras* in Professor Gregory's collection that were described by Spath (1922). All these collections, and two smaller ones, also contain many examples of the well-known Upper Albian ammonites of Angola described by Spath, Haas and others, but none of them belongs to undescribed species or warrants further description.

Acknowledgements. Loans of type or figured specimens or of plaster casts of type specimens were kindly made available by Carlos A. Neves Ferrão, Director of the Serviços de Geologia e Minas, Luanda, Dr. N. P. Newell, of the American Museum of Natural History, New York, Dr. L. Cahen, Director of the Musée royal de l'Afrique centrale, Tervuren, Dr. A. W. Crompton, Director of the South African Museum, Cape Town, and Dr. J. Sornay of the Muséum national d'histoire naturelle, Paris. Mr. C. W. Wright made some helpful suggestions on the species of *Baculites* discussed. The majority of the photographs were taken by the author, but a few of the larger specimens were taken by Mr. N. Tanti.

Measurements. Whorl dimensions are quoted in millimetres in the following order: Diameter: whorl height, whorl breadth, width of umbilicus. Figures in brackets following each of the last three figures express that figure as a proportion of the diameter.

II AMMONITE FAUNAS OF THE MARINE CRETACEOUS OF ANGOLA

A complete bibliography of Angolan geology can be found in Andrade & Andrade (1958) and a bibliography of the Jurassic and Cretaceous rocks in Haughton (1959). General accounts of the Cretaceous of Angola are available in Mouta (1954: 53–58) and Haughton (1963: 277–283). Cretaceous sediments are confined to the coastal strip of Angola and stretch from Moçâmedes in the south to Cabinda in the north.

Except in the Cuanza basin where the width reaches 140 km., the strip is nowhere more than a few kilometres wide. Along the whole coastal strip lagoonal and continental deposits of Aptian or pre-Aptian age rest directly on the basement complex. Marine conditions first appear towards the top of the Aptian and a thick series of sediments (attaining 2000 metres in places) was laid down, containing representatives of all the stages up to the top of the Cretaceous. The marine beds of this coastal strip can conveniently be divided into five basins (Neto 1961: 63). Ammonites have not been found in the two northerly basins of Cabinda and Congo, but occur in considerable numbers in the Cuanza, Benguela and Moçâmedes basins.

(a) *Moçâmedes basin.* The general succession in this small southerly basin is as follows (Carvalho 1960: 37–48; 1961: 27-93, 210-212; Haughton 1963: 278–279):

8. Maastrichtian. Fauna of fish teeth.
7. Santonian or Campanian.
6. Basalt.
5. Cenomanian. Limestone with concretions.
4. ?Albian. White Limestone.
3. Unfossiliferous sandstone.
2. Conglomeratic facies of torrential origin.
1. Lagoonal facies.

Lamellibranchs and gastropods are common in divisions 4, 5 and 7 and have been described by Rennie (1929; 1945), but the ages of the lower two were wrongly stated to be Senonian. From a single bed only 0·4 metres thick in the upper part of division 5 at Salinas came the fine ammonite fauna described by Douvillé (1931). Spath (1931: 316; 1932*a*: 124) reviewed the determinations of those ammonites and established that, contrary to Douvillé's assertions that Barremian to Turonian forms were represented, all were Cenomanian in age. A single specimen from Salinas was figured by Haas (1952: 2–4, figs. 3, 4) as *Desmoceras latidorsatum* (Michelin), var. *inflata* Breistroffer, and referred to the Albian. Its position in the succession at Salinas is not known. It agrees closely with species of known Albian age in the Benguela basin, but the species and variety occur in both the Upper Albian and Lower Cenomanian in other areas, so it may have been part of the Cenomanian fauna at Salinas described by Douvillé. The only other ammonite known from the succession of this basin is the specimen from division 7 at San Nicolau recorded as *Baculites* aff. *asper* (Morton) by Spath (1951: 9), which is not specifically determinable and may be Santonian or Campanian.

(b) *Benguela and Cuanza basins.* The succession in the Benguela basin has been described by Neto (1960: 89–99; 1961: 63–93) and Haughton (1963: 279–281), and stratigraphical descriptions and maps for the Cuanza basin can be found in Brognon & Verrier (1958: 61–74), Hoppener (1958: 75–82) and Freneix (1959: 111–113). The succession and ammonite faunas of both basins are similar and may be considered together.

1. *Albian.* The celebrated Albian ammonite fauna of Angola is known mainly from localities close to Benguela. Important early works on the stratigraphy and ammonites of the Albian of that region by Choffat (1888; 1905) and Gregory (1916;

1922) were summarized and expanded by Spath (1922) when he described an extensive collection made by Professor Gregory. Further Albian collections were described by Haughton (1925), Airachi (1931), Thiele (1933) and Haas (1941). The whole of the previous work was again summarized by Haas (1942) when he described a large collection from the Albian of Hanha. Further Albian ammonites have been described by Haas (1945; 1952—but some are Campanian and are listed below), Sornay (1951; 1953) and Soares (1959). Almost the whole of this Albian fauna is of Upper Albian age. It is rich in specimens of *Hysteroceras*, *Neokentroceras*, *Mortoniceras*, *Elobiceras*, *Puzosia* and Hamitidae, of which the lowest in the succession are *Hysteroceras* and *Neokentroceras* (see p. 400 below) and date the base of the series as low in the Upper Albian. Specimens of *Stoliczkaia* figured by Choffat (1888: 69, pl. 2, figs. 5–9) and recorded by Haughton (1925: 270) and Mouta & O'Donnell (1933: 63) (none were seen by Spath or Haas) occur in beds above the main *Mortoniceras* bearing beds, and led to the proposal (Mouta & O'Donnell 1933: 58–63; Mouta 1954: 128) of a formation characterized by *Stoliczkaia*. This is still Upper Albian in age, probably the upper half. (A *Stoliczkaia* figured by Douvillé (1931: 29, pl. 2, fig. 2) from the Salinas fauna is almost certainly Cenomanian, like the remainder of Douvillé's ammonites). Beds below the Upper Albian succession contain specimens of *Douvilleiceras* and *Puzosia* in some abundance (Neto 1960: 96; 1961: 69), indicating a Lower Albian age, but only one of the examples of *Douvilleiceras* has ever been figured (Choffat 1888: 71, pl. 3, fig. 1). In the collections with which the present paper is concerned there are examples of most of the Upper Albian genera, but nothing new, except in the case of *Neokentroceras*, which is represented by a splendid series of specimens that are described in detail below and greatly extend our knowledge of this genus. A small collection of *Douvilleiceras* is also described, which establishes the age of the beds from which they come as Lower Albian.

2. *Cenomanian—Santonian*. All the stages of the Upper Cretaceous are probably present in the Cuanza basin (Brognon & Verrier 1958) and ammonites from most of them have been mentioned by Hoppener (1958: 79–81). A Cenomanian *Acanthoceras* and a Turonian *Mammites* were recorded by Thiele (1933), and Haas (1942*a*) described two poorly preserved ammonites, ?*Mantelliceras* and *Sharpeiceras goliath*, that are probably Cenomanian, a poor Turonian ?*Romaniceras*, and three well preserved *Texanites* of Santonian age. An Upper Santonian *Placenticeras*, *P. reineckei*, was figured by Haughton (1925: 271, pl. 13, figs. 4, 5). More recently Basse (1963: 871–875, pls. 22–24) has described a new collection of Upper Turonian–Lower Coniacian ammonites from Cape Ledo, Cuanza basin, which consists of examples of *Prionocyclus* and *Subprionocyclus*, and the new genus *Ledoceras*. Nothing comparable with the excellent Cenomanian ammonites of the Moçâmedes basin has been found in the Benguela or Cuanza basins.

3. *Campanian and Maastrichtian*. The presence of ammonites of these two stages has often been mentioned, but only a few have been described hitherto. Their first mention was by Spath (1921: 56), referring to the Barra do Dande *Nostoceras* collected by Beeby Thompson that are described herein. The first to be described and figured were Haughton's (1925) Campanian and Maastrichtian ammonites from

Carimba, consisting of species of *Nostoceras*, ?*Didymoceras*, ?*Solenoceras*, *Baculites*, *Menuites* and *Libycoceras*. Further ammonites from the Carimba district and from Capolo were described by Haas (1943), all consisting in this case of the heteromorphs *Nostoceras*, *Axonoceras*, *Solenoceras*, and *Baculites*. Preliminary identifications of the Campanian and Maastrichtian ammonites described herein were given by Spath (1951; 1953: 49, 50). Two fine specimens of *Nostoceras* from Barra do Dande were figured by Sornay (1951), and a fragment of a large *Didymoceras* from the same locality was figured by Silva (1961). All the above ammonites are from the Cuanza basin, but a Campanian succession also occurs in the Benguela basin, especially at Egito. Part of the Egito Campanian ammonite fauna was described unwittingly by Haas (1952) and wrongly referred to the Albian. Haas (1952: 16) said "the Albian age of the Ammonoidea here described is beyond any doubt", but at Egito, Campanian beds lie unconformably on Upper Albian, and ammonites from the Egito Campanian were mixed in his descriptions with Albian ammonites from other localities. "*Puzosia lytoceroides*" Haas (1952: 8–11, figs. 14–17) is the Upper Campanian form *Gaudryceras varagurense* (Kossmat), "*Gaudryceras aenigma*" Haas (1952: 11–12, figs. 18–20) is *Anagaudryceras mikobokense* Collignon, and the smaller of the two specimens figured as *Tetragonites jurinianus angolana* Haas (1952: 12–15, figs. 21, 23–25 only) is probably Campanian and is best identified as *Tetragonites* cf. *epigonus* (Kossmat). The other ammonites described by Haas are all from Albian localities in the Benguela region, the only doubtful ones being the four Egito specimens listed as *Desmoceras latidorsatum* (Michelin) var. *inflata* Breistroffer (Haas 1952: 3, 4), none of which was figured. Measurements of these four given by Haas agree with those of the Albian Catumbela specimens, and it is doubtful whether anything in the Campanian has such thick and depressed whorls, so their reference to the Albian species is probably correct.

The rich Campanian and Maastrichtian collections from Egito and Barra do Dande that were summarized by Spath (1951) are described below, and there are smaller faunas from the Senonian of Carimba, Benguela and San Nicolau. The collection is richer than any Upper Cretaceous ammonites previously described from Angola.

III SYSTEMATIC DESCRIPTIONS

Family **DOUVILLEICERATIDAE** Parona & Bonarelli 1879

Genus ***DOUVILLEICERAS*** Grossouvre 1894

Douvilleiceras mammillatum (Schlotheim) ? var. ***aequinodum*** (Quenstedt)

Plate 1, figs. 1–4

1846 *Ammonites monile aequinodus* Quenstedt: 138, pl. 10, fig. 2.
1888 *Acanthoceras mamillare* (Schlotheim); Choffat: 71, pl. 3, fig. 1.
1925 *Douvilleiceras monile* (J. Sowerby); Spath: 73, pl. 5, fig. 5.
1962 *Douvilleiceras mammillatum* (Schlotheim) var. *aequinodum* (Quenstedt); Casey: 271, pl. 40, fig. 5, pl. 41, figs. 5–7, pl. 42, fig. 10.

Material. 8 specimens, D.G. 294, 300, 306–309, 312 and 322, from Dombe Grande, Benguela basin, in the collection of the Serviços de Geologia e Minas, Luanda.

Description. The collection consists of four complete specimens, the largest being 63 mm. diameter, and four fragments of less than half a whorl. The whorl section is depressed in all specimens, with a height/breadth ratio of 0·75 to 0·80. There are 28 to 30 ribs per whorl at 60 mm. diameter. Up to about 40 mm. diameter all the ribs appear to commence at the umbilical edge, but at larger diameters about one-third are intercalated and commence only very weakly at the umbilical edge or in the middle of the side of the whorl. The ribs on all whorls are inclined slightly backwards. Each rib bears seven tubercles on each side of the whorl, which are equal in size and approximately evenly spaced after 45 mm. diameter. The largest specimen has an eighth tubercle on ribs near its aperture. At sizes smaller than 45 mm. diameter a much larger single lateral tubercle occurs on alternate ribs. These ribs have a small umbilical tubercle, the large lateral tubercle and three small ventro-lateral tubercles, and the ribs with which they alternate bear 5 or 6 small tubercles. At sizes smaller than 25 mm. diameter the large lateral tubercle appears to be developed on every rib. The mid-ventral sulcus is only a slight depression in the ribs which are continuous across the venter; it is roughly equal to the distance between the first and third ventro-lateral tubercles. Only poor traces of septa and suture-lines are to be seen in the specimens, but the three largest complete examples appear to have about two-thirds of a whorl of body chamber each, and are presumably immature.

Measurements of the four best examples are as follows:

D.G. 294. ———: 24·0, 29·9, ——.
D.G. 306. At 58 mm.: 24·1 (0·42), 29·2 (0·50), 20·6 (0·36).
D.G. 308. At 58·6 mm.: 24·0 (0·41), 29·7 (0·51), 19·0 (0·32).
D.G. 309. At 55·2 mm.: 22·6 (0·41), 28·2 (0·51), 18·3 (0·33).

Remarks. The full synonymy of *Douvilleiceras mammillatum* (Schlotheim) and its varieties has been given by Casey (1962: 265–274). The present Angolan specimens are referred to var. *aequinodum* of that species rather than to the type variety because of the fairly high rib density of 28 to 30 ribs at 60 mm. diameter. The development of a large lateral tubercle up to 45 mm. diameter and the relatively wide ventral sulcus are more like the type variety of the species, while the umbilical width could be that of either variety when compared with Casey's (1962: 267, 271) measurements. The strength of the ribs is variable in the Angolan specimens due to the varying preservation, but in some places the ribs are as strong and wide as in typical English and French examples of the species.

The only previously figured Angolan *Douvilleiceras* (Choffat 1888: 71, pl. 3, fig. 1) shows exactly the same characters as the present collection and is here referred to the same species and variety. It has the large lateral tubercles on the inner whorls and is drawn with eight tubercles on each rib near its aperture at about 70 mm. diameter.

In Britain and France this species is confined to and characterizes the Mammillatum Zone, the upper half of the Lower Albian. The species also occurs in Madagascar (e.g. Besairie 1936: 158, fig. 10*b*; Collignon 1949: 76; 1950: 46; 1963: figs. ?1238, ?1239, 1241, ?1242, ?1248) where its stratigraphical position, characterizing a zone at the top of the Lower Albian, is again accurately known (Besairie & Collignon 1956: 32–36; 1960: 68–74). The only other record from Africa is of specimens from Somalia recorded and figured by Tavani (1942: 33, pl. 3, fig. 10; 1949: 37).

Douvilleiceras orbignyi Hyatt

Plate 1, fig. 5

1841 *Ammonites mammillaris* Schlotheim; d'Orbigny: 249, pl. 73, figs. 1–3.
1903 *Douvilleiceras orbignyi* Hyatt: 110.
1923 *Douvilleiceras mammillatum* (Schlotheim) var. *baylei* Spath: 70, pl. 5, fig. 4.
1962 *Douvilleiceras orbignyi* Hyatt; Casey: 279, pl. 40, figs. 6–8, pl. 42, figs. 12, 13.

MATERIAL. One specimen, D.G. 305, from Dombe Grande, Benguela basin, in the collection of the Serviços de Geologia e Minas, Luanda.

DESCRIPTION. The specimen consists of a half whorl fragment of about 50 mm. maximum diameter. The whorl section is greatly depressed, the whorl height and breadth being 17·5 and 25·6 mm. respectively near the aperture. Very large ventro-lateral tubercles, each divided by three spiral ridges, define a deep U-shaped mid-ventral sulcus. Large spinose mid-lateral tubercles occur on alternate ribs and below these there are tiny umbilical tubercles. Just before the broken aperture there is a single low rib with small tubercles; otherwise the ribbing is very weak throughout.

REMARKS. This single specimen agrees with typical English and French examples of *D. orbignyi* at similar sizes. It is readily distinguished from any of the varieties of *D. mammillatum* by the large ventro-lateral tubercles. *D. orbignyi* has these tubercles without, or with very few, intermediate small ribs. *D. alternans* Casey differs in having one intermediate rib at 50 to 100 mm. diameter, and *D. magnodosum* Casey and *D. inaequinodum* (Quenstedt) both have two intermediate ribs at similar sizes. These characters appear to be constant in these species, although there is considerable variation in other details of the ornament. In *D. orbignyi* the size of the lateral and ventro-lateral tubercles and the size of the ribs show much variation amongst the French neotype and topotypes and English specimens figured by Casey (1962: 279, figs. 99, 100, pl. 40, figs. 6–8, pl. 42, figs. 12, 13). The Angolan specimen has weak ribs more like the neotype than some of the other figured examples. The Madagascan species *D. benonae* Besairie (1936: 164, pl. 15, figs. 15, 16; Collignon 1963, fig. 1244) has even larger ventro-lateral tubercles and many more intermediate ribs.

In Britain and France *D. orbignyi* is an associate of *D. mammillatum* in the Mammillatum Zone. Several specimens are known from Madagascar from the same zone at the top of the Lower Albian (Besairie 1936: 160; Collignon 1949: 76; 1950: 46; 1963: figs. ?1240, 1248).

Family **BRANCOCERATIDAE** Spath 1933

Subfamily **BRANCOCERATINAE** Spath 1933

Genus ***NEOKENTROCERAS*** Spath 1921

TYPE SPECIES. *Neokentroceras curvicornu* Spath 1921.

EMENDED DIAGNOSIS. Small size; largest known adult is 40 mm. diameter when complete. Evolute, whorl section quadrilateral or rounded-quadrilateral. Ribs weak or absent in most species, but moderately strong in some. Umbilical tubercle strong; lateral tubercle weak or absent; ventro-lateral tubercle strong, clavate or spiny, but is sometimes absent when ribbing is strong. Keel present in all species. On final part of the adult body chamber the ventro-lateral tubercles become replaced by high ribs which curve strongly forwards to form continuous folds across the venter, and the keel is almost completely lost.

AGE AND DISTRIBUTION. Lower half of the Upper Albian. Angola, ? Nigeria, ? Brazil.

REMARKS. The first proposal of *Neokentroceras* (Spath 1921*a*: 306) consisted merely of four words of description and the designation of a type species which was a *nomen nudum*. In a paper the following year Spath (1922: 105–107, 139–143, text-fig. D) gave full descriptions and discussion of the genus, its type species, and three further new species. Only 21 specimens were available to Spath; of these, 6 were not described (these are *N. trituberculatum* sp. nov. described below), and only 4 out of the remaining 15 were reasonably complete specimens. Spath's poor illustrations made interpretation of the genus and its species very difficult for later workers except by reference to his original specimens.

A second collection of *Neokentroceras* from Angola was described at length by Haas (1942: 46–66, pls. 7–10). It consisted of 117 specimens, of which all except about 9 were fragments of less than half a whorl. Haas adopted the 4 species and 1 variety of Spath and proposed a further 4 species and 4 varieties.

The only other discussion of this genus is Reyment's (1955: 39–41) description of three Nigerian specimens, which were referred to the type species of the genus, but two of them were made the type specimens of a newly created subspecies.

The present collection yields a considerable amount of new information on *Neokentroceras*, for, although there are only 48 additional specimens, 33 of them are fairly complete and 20 have adult body chambers or adult suture-lines preserved. All are from a single locality at Praia do Jombo, Benguela basin, Angola. There are several specimens in each of the species described below which are complete up to the adult mouth border, and they all show a similar type of modification of the ornament on the final part of the body chamber. The ribs on the side of the whorl strengthen in all cases; where ventro-lateral tubercles are present they diminish in size and lose much of their tuberculate nature to become merely raised portions of the ribs; the ribs form chevrons or folds that are continuous across the venter, and the keel diminishes markedly, almost disappearing in many cases. In all instances where the final suture-lines and the modified ornament on the body chamber are seen in the same specimen, the final suture-lines are approximated.

The most highly developed species of *Neokentroceras* is the heavily tuberculate type species, *N. curvicornu*, which has characters that are clearly different from any other genus of comparable age. The two ribbed species *N. pseudovaricosum* Spath and *N. crassicostatum* sp. nov., are, on the other hand, not far removed from some species of *Hysteroceras*. Amongst the Angolan forms *Hysteroceras varicosum* (J. Sowerby) var. *angolana* Haas (1942: 21–24, pl. 1, fig. 21, pl. 2, figs. 1–17) bears considerable resemblance to the ribbed species of *Neokentroceras*. Small inner whorls of *N. pseudovaricosum* and *H. varicosum* var. *angolana* are so alike as to be virtually indistinguishable, and it is probable that the two species are closely related. *Hysteroceras orbignyi* (Spath), a well-known species of the English Gault which is also found in Angola, is related to ribbed species of *Neokentroceras*. In all species of *Hysteroceras* the keel rapidly disappears and the ribs are continuous across the venter on most or all of the body chamber, whereas in *Neokentroceras* this stage is only reached on a short portion of the adult body chamber just before the mouth border.

In view of the characters of the adult *Neokentroceras* that are now known, the two Nigerian specimens figured as the new subspecies *N. curvicornu crassicornutum* by Reyment (1955: 41, pl. 4, figs. 7, 8) cannot be placed in this genus. The smaller specimen (pl. 4, fig. 8) has large swollen ventro-lateral tubercles, small lateral tubercles and umbilical tubercles, while the larger specimen (pl. 4, fig. 7) shows a larger body chamber (? adult) with a broad flat venter and a strong keel, and quadrituberculate main ribs and some trituberculate intercalated ribs that do not reach the umbilical edge. These are clearly characters of the subgenus *Mortoniceras* (*Durnovarites*) to which both Reyment's specimens should be referred, as *M.* (*D.*) *crassicornutum*, a species with particularly large ventro-lateral tubercles on the inner whorls. Reyment's third specimen (1955: 41, pl. 4, figs. 9, 9*a*), from a slightly lower horizon and preserved in a different matrix, is a fragment of a whorl which may well be a genuine *N. curvicornu*. From the body chamber characters of the largest specimen referred to above, Reyment (1955: 39) deduced that *Neokentroceras* was related to the quadrituberculate forms of *Mortoniceras*, a relationship first suggested by Spath (1922: 106). This is not correct for the proper adult characters now known for *Neokentroceras* point strongly to this genus being a late end-form development from *Hysteroceras*, a view adopted later by Spath (1934: 472–473) and also by Haas (1942: 47–48). Its age is therefore low in the Upper Albian. *Neokentroceras* should be referred to the subfamily Brancoceratinae rather than to the Mortoniceratinae, for it is unlikely to have had any direct connections with members of the latter family.

Records of *Neokentroceras* indicating a world-wide distribution were listed by Spath (1922: 105–107) and by Haas (1942: 46–47). Spath's (1934: 472) later view, that the genus was restricted to Angola, seems to be more correct, for records of the genus from Texas, Tunisia, India and Borneo are all based on figured specimens which are examples of *Mortoniceras* (s.l.), *Spathiceras* or *Dipoloceras*. The single specimen from Nigeria figured by Reyment (1955: pl. 4, figs. 9, 9*a*) appears to be a genuine *Neokentroceras*, and the record of *N. tectorius* (White 1887: 225, pl. 20, figs. 6, 7) from Brazil, based on a diagrammatic drawing of a single specimen, is doubtful. Thirteen specimens from the Upper Albian of Madagascar figured by Besairie (1931: 633, pl. 65, figs. 4–7) and Collignon (1932: 16–17, pl. 3, figs. 1–9) are close to *Neokentroceras*. However they are all inner whorls of less than 15 mm. diameter, ribs are present in all cases together with small umbilical and ventro-lateral tubercles, and on the venters of even the most tuberculate specimens the keel is always dominant over the ventro-lateral tubercles. Their reference to *Hysteroceras* is more logical, for several of them are close to the more tuberculate examples of *H. orbignyi* Spath and *H. binum* (J. Sowerby) from the English Gault. Thus apart from possible occurrences in Nigeria and Brazil, there do not appear to be any records of genuine *Neokentroceras* from outside Angola.

The present division of *Neokentroceras* into species is unsatisfactory, owing to the poor illustrations in Spath's (1922) original paper, and to the fragmentary nature of nearly all the specimens described by Haas (1942). The collection described here contains the first complete specimens to be found. Haas's division into 8 species and 5 varieties is excessive for many of his forms can be seen to represent individual variation within a species amongst the present collection. The amount of variation within one species is well illustrated in the 7 specimens of *N. pseudovaricosum* described and figured below (Pl. 3, figs. 5–11). They show variation in adult size giving a factor of nearly 2:1 between the largest and smallest, and marked variation in rib density and whorl thickness. There are four or five different combinations of adult size, rib density and whorl thickness, yet all are united by the possession of highly characteristic ribs, which are broad and flattened at the ventro-lateral edge. It is clearly more correct to unite these under one specific name than to divide them into 4 or 5 species. Similar amounts of variation are found amongst the 29 specimens of *N. curvicornu*, and the smaller numbers of other species. In the collection as a whole divisions can be made at natural breaks in the variation, except in one case where two species seem to be very close, and the result is that only four of the previously described species are recognized and two new species are described.

Neokentroceras curvicornu Spath

Plate 2, figs. 1–9

1921*a* *Neokentroceras curvicornu* Spath: 306 (*nomen nudum*).
1922 *Neokentroceras curvicornu* Spath: 139–140, figs. D 1, 1*a*, 2.
1942 *Neokentroceras speciosum* Haas: 61-63, figs. 6*n*, *o*, pl. 8, figs. 14–17, pl. 9, fig. 10.
1942 *Neokentroceras speciosum* var. *rudis* Haas: 63, fig. 6*p*, pl. 8, figs. 18, 19.
?1955 *Neokentroceras curvicornu curvicornu* Spath; Reyment: 41, pl. 4, figs. 9, 9*a*.

HOLOTYPE. C. 20116 (Pl. 2, fig. 1).

MATERIAL. In addition to the holotype, 28 specimens, including four paratypes (C. 20117–18, C. 20123, C. 20289) from the shore at landing place near Hanha, and C. 52551–54, C. 52556–73, C. 52575 and C 52584 from Praia do Jombo. Dimensions of holotype: at 24 mm.: 7·7 (0·32), ——, 10·0 (0·41). Dimensions of C. 52552: at 26·5 mm.: 9·0 (0·34), 8·3 (0·31), 11·6 (0·44).

Diagnosis. Evolute, whorl section quadrilateral, thickness and height of whorl approximately equal. Umbilical tubercle large and radially elongated. Ventrolateral tubercle very large and forms outwardly pointing spine, sometimes curved slightly backwards. Keel well formed but lower than tubercles in all cases. Ribs weak or absent, except on final part of body chamber where tubercles diminish markedly in size, the keel disappears and the ribs are projected on the venter to form large folds. Length of adult body chamber about five-eighths of a whorl.

Remarks. The holotype was badly figured by Spath, but the specimen is poorly preserved and from the figure given here (Pl. 2, fig. 1) it can be seen that the specific characters are barely discernible. However, the collection contains 24 specimens in addition to those seen by Spath, and as many of these are well preserved and show all stages of growth, the species can now be adequately described.

Ten specimens have recognizable adult features, and these have mouth borders at sizes ranging from 21 to 35 mm. diameter, and approximated last suture-lines at diameters between 14·5 and 20·5 mm. Modification of the ornament on the adult body chamber consists of a tendency for the last three pairs of ventro-lateral tubercles to become elongated and to join across the venter as high forwardly curving ribs, and at this stage the keel almost disappears. On the middle one-third of the length of the adult body chamber the ventro-lateral tubercles become elongated into very large and widely spaced spines, but there is considerable variation in the degree of coarseness attained and in the direction of the spines, some of which are straight while others curve backwards even in the same specimen.

The tubercles on the first one-third of the body chamber and the preceding septate whorls are fairly constant in size and density. At diameters between 20 and 28 mm. the numbers of ventro-lateral and umbilical tubercles average 15 and 10 per whorl respectively, and only on occasional specimens do these figures rise as high as 18 and 12. On the holotype there are 13 ventro-lateral and 10 umbilical tubercles per whorl at 27·3 mm. diameter, and the low figure of 13 reflects the wide spacing of the ventro-lateral tubercles on the last quarter whorl. It is probable that this part of the holotype is the middle one-third of the length of the body chamber, but this cannot be confirmed by the suture-lines which are not preserved. Lateral tubercles are not found at any stage of growth.

Rib development is weak. The umbilical and ventro-lateral tubercles are sometimes joined by a rib at the beginning and end of the body chamber, but these always show loss of relief when crossing the side of the whorl, and on other parts of the whorls ribs are absent or only very weak. The keel is small and is always lower than the ventro-lateral tubercles.

This is the most evolute and most strongly tuberculate species of *Neokentroceras*, in which the development of keel and ribs is always very weak in comparison with the tubercles. *N. singulare* Haas is closely related and is discussed in detail below.

N. trituberculatum sp. nov. is also similar but develops a lateral tubercle from an early growth stage.

N. speciosum and its variety *rudis* described and figured by Haas (1942) are synonyms of *N. curvicornu*. His specimens all fall well within the range of variation of the latter species. The holotype of *N. speciosum* (Haas 1942, pl. 8, fig. 14) is close to the adult growth stage, and compares well with the specimen figured in Pl. 2, fig. 7. The type specimen of var. *rudis* (Haas 1942: pl. 8, fig. 18) can also be matched amongst the present collection (it is fairly close to Pl. 2, fig. 3), and the varietal name is not worth retaining. The three specimens figured by Haas (1942, pl. 8, figs 20–22) as *N. curvicornu*? are small fragments which are not really specifically determinable.

Three Nigerian specimens were figured by Reyment under this specific name. One of them (Reyment, 1955: pl. 4, figs. 9, 9*a*) compares well with the specimen figured here in Pl. 2, fig. 9, and although fragmentary and poorly preserved it is probably a genuine *N. curvicornu*. The other two specimens (Reyment, 1955: pl. 4, fig. 7, 8) were made the types of the new subspecies *N. curvicornu crassicornutum:* this has been discussed above (p. 347) and shown to be probably a valid species of *Mortoniceras* (*Durnovarites*).

Neokentroceras singulare Haas
Plate 2, figs. 10–15

1942 *Neokentroceras singulare* Haas: 64–66, fig. 6*r*, *s*, pl. 9, fig. 11, pl. 10, fig. 1.

MATERIAL. 14 specimens, C. 52555, C. 52574, C.52576-83, C. 52585-87 and C. 52597 all from Praia do Jombo.

DIAGNOSIS. Close to *N. curvicornu*, but distinguished by being slightly more involute, with flat and smooth whorl sides, and more compressed whorl shape. Umbilical tubercles of moderate size; ventro-lateral tubercles large and elongated into spines curving backwards. Ribs weak throughout. Adult body chamber similar to *N. curvicornu*.

REMARKS. If a much larger collection were available, a complete gradation might be found between this species and *N. curvicornu*, and *singulare* would then be considered a variety of the latter species. There are sufficient distinguishing features in the present collection of only 14 specimens, however, to justify their separation from *N. curvicornu* as a distinct, but very closely related species. At all stages the whorls are more compressed and a little more involute than in *N. curvicornu*. The sides of the whorl are nearly smooth in most individuals, and the tubercles are somewhat smaller than in the latter species.

In the seven specimens that show adult characters, the diameter at the mouth border ranges from 23 to 35 mm., and the diameter at the final approximated suture-lines ranges from 15·5 to 22 mm. The body chamber occupies five-eighths of a whorl and has modifications of the ornament similar to those in *N. curvicornu*, i.e. the ventro-lateral tubercles are large and widely spaced on the middle part of the body chamber, and just before the mouth border the last 3 or 4 tubercles are modified to form raised ribs which curve forwards and cross the venter as folds (Pl. 2, figs. 11, 15).

On the septate whorls and the beginning of the body chamber the sides of the whorls are flat and almost smooth and neither the umbilical nor the ventro-lateral tubercles project markedly outwards from the side of the whorl as in *N. curvicornu*. Ribbing is very weak on these whorls and only occasionally do low ribs join the umbilical and ventro-lateral tubercles. On whorls between 20 and 25 mm. diameter there are 10–12 umbilical and 15–18 ventro-lateral tubercles per whorl, but the number of the latter may fall to 13 if the middle part of the adult body chamber is included. Lateral tubercles are never developed. The keel is about as high as the ventro-lateral tubercles on the septate whorls, but diminishes on the body chamber and disappears just before the mouth border.

The single specimen and holotype of the species described by Haas (1942, pl. 10, fig. 1) appears to be an almost complete adult, for it has ribs just before the aperture which cross the venter as folds. The mouth border is just missing and the maximum size when complete would have been about 25 mm. diameter. It is very closely matched by the complete adult figured here in Pl. 2, fig. 15.

Neokentroceras subtuberculatum Spath

Plate 3, fig. 1

1888 *Schloenbachia lenzi* Szajnocha; Choffat: 64, pl. 1, fig. 3 (non figs. 4–6).
1922 *Neokentroceras subtuberculatum* Spath: 141–142, figs. D 8, 8*a*.
1922 *Neokentroceras choffati* Spath: 106.
?1942 *Neokentroceras choffati* Spath; Haas: 49–51, fig. 6*a*, pl. 7, figs. 15–18, pl. 9, fig. 4.
1942 *Neokentroceras choffati* Spath var. *crassinoda* Haas: 50, pl. 7, fig. 19.
1942 *Neokentroceras costatum* Haas: 52–53, figs. 6*b–d*, pl. 7, figs. 20–25, pl. 9, fig. 5.
1942 *Neokentroceras magnum* Haas: 53–56, fig. 6*g*, pl. 8, figs. 2–6, pl. 9, fig. 6.
1942 *Neokentroceras* cf. *subtuberculatum* Spath; Haas: 56–58, figs. 6*h*, *i*, pl. 8, fig. 7, pl. 9, fig. 7.

HOLOTYPE. C. 20042 (Pl. 3, fig. 1), the only specimen, from near Benguela.

REMARKS. The species is poorly known, but the two diagnostic features appear to be the development of ribs throughout growth and a small lateral tubercle on the adult body chamber, in addition to small umbilical tubercles and moderate sized ventro-lateral tubercles.

The holotype was so badly figured by Spath that the species could not be properly interpreted from his descriptions. The specimen is, in any case, poorly preserved, and a full description of the species will only be possible when complete, well-preserved specimens are found. A second specimen, C. 20061, which was referred to this species by Spath is very badly preserved and is specifically indeterminate.

The only part of the holotype that is at all well preserved is the final half whorl. This is probably part of the adult body chamber, though it is not possible to prove this as no suture-lines are preserved and the mouth border is missing. On this part of the specimen the whorl shape is quadrangular, slightly higher than broad, and has parallel, almost flat sides. The umbilical tubercles are small and radially elongated, while the ventro-lateral tubercles are of medium size and point outwards, and have a tendency to be clavate. Small lateral tubercles are connected to both the inner and outer tubercles by low ribs. In some cases the radial elongation of the umbilical tubercle is angled slightly forwards on the ventral side of the tubercle, and the rib commences from the middle of the tubercle and runs behind this elongation. On other ribs the elongation is part of the rib itself. There are 18 ventro-lateral tubercles on the final whorl at about 35 mm. diameter; the number of umbilical tubercles is less than this, but an accurate count cannot be made owing to the poor preservation.

The holotype of *N. choffati* Spath was figured by Choffat (1888: pl. 1, fig. 3). This shows all the characters typical of *N. subtuberculatum* and there can be little doubt that it is a synonym. The specimens figured as *N. choffati* by Haas are all too small to be referred with certainty to the present species, though this will probably be possible when the septate whorls of *N. subtuberculatum* are properly known. The variety *N. choffati* var. *crassinoda* and the two species *N. costatum* and *N. magnum* of Haas are also included in the synonymy of *N. subtuberculatum*. A collection of more complete specimens will be necessary to confirm this synonymy, but the characters of the fragments figured and described under these names agree closely with those of *N. subtuberculatum*.

Neokentroceras trituberculatum sp. nov.
Plate 3, figs. 2–4

HOLOTYPE. C. 20285 (Pl. 3, fig. 2).

MATERIAL. In addition to the holotype, five paratypes, C. 14818-21, C. 20284 all from near Catumbella, Benguela, Angola.

DIAGNOSIS. Whorls robust with quadrangular section. A lateral tubercle of moderate size occurs in addition to a moderate-sized umbilical tubercle and a large clavate ventro-lateral tubercle. Ribs weak throughout and often absent on septate whorls. Keel well formed but lower than ventro-lateral tubercles.

REMARKS. The six specimens referred to this species form part of a collection purchased from Dr. W. J. Ansorge, and they have been referred to by Spath (1922: 140) and Reyment (1955: 39). The specimen C. 36204 referred to by Reyment (1955: 39) as belonging to a related but different trituberculate species, is only 16 mm. diameter, and consists of small inner whorls of *Mortoniceras* (*Durnovarites*), as was recognized by Spath (1942: 713).

This species is characterized by a well developed lateral tubercle which is placed slightly ventral of the middle of the side of the whorl and is developed from an early stage of growth. The umbilical tubercles are sharp and pointed on the inner whorls, becoming radially elongated on later whorls, while the ventro-lateral tubercles are large and tend to become clavate. Weak ribs are developed between the tubercles on the adult body chamber, but on the septate whorls they are still weaker or absent.

The holotype is septate up to 25 mm. diameter, but owing to the preservation it cannot be determined whether the final suture-lines are approximated; these are followed by five-eighths of a whorl of body chamber ending at a maximum diameter of 37·5 mm. This specimen is not quite complete, but has a small portion of the umbilical wall part of the mouth border preserved, indicating a diameter of 40 mm. when complete. The ornament on the side of the whorl shows no significant modification towards the end of the body chamber and the venter at this point is poorly preserved. There are 16 ventro-lateral and 15 umbilical tubercles on the last whorl at 38 mm. diameter. C. 20284 is a second large specimen having a maximum diameter of 38 mm., but the preservation is such that no suture-lines can be seen. It has 16 ventro-lateral and 16 umbilical tubercles on its final whorl. Specimens C. 14818–21 are parts of the inner whorls of four individuals; they all have maximum diameters between 15 and 19 mm. and suture-lines are only preserved in one specimen. The lateral tubercle first appears at about 14 mm. diameter in these specimens, at which size the umbilical and ventro-lateral tubercles are well developed.

All other species of *Neokentroceras*, except *N. subtuberculatum*, differ in having no lateral tubercles. *N. subtuberculatum* differs in having smaller lateral tubercles that only appear at later growth stages and in having stronger ribs.

Neokentroceras pseudovaricosum Spath

Plate 3, figs. 5–11

1922 *Neokentroceras pseudovaricosum* Spath: 142, fig. D 4, 5, 5*a*.
1922 *Neokentroceras pseudovaricosum* var. *compressa* Spath: 142, fig. D 6.
1942 *Neokentroceras costatum* var. *tenuis* Haas: 53, figs. 6*e*, *f*, pl. 7, figs. 26, 27, pl. 8, fig. 1.

HOLOTYPE. C. 20125 (Pl. 3, fig. 5), from the shore landing place near Hanha.

MATERIAL. In addition to the holotype, 6 specimens; C. 20120, C. 20122 (paratypes), C. 20124 from the shore at landing place near Hanha, and C. 52590–92 from Praia do Jombo.

Dimensions are as follows:

C. 20125.	At 21·0 mm.: 7·0 (0·33), 6·6 (0·31), —. At 18·9 mm.: 6·5 (0·34), 6·0 (0·31), —.
C. 20120.	At 15·7 mm.: 6·2 (0·39), 5·6 (0·35), —.
C. 20122.	At 21·0 mm.: 7·8 (0·37), 7·0 (0·33), —.
C. 20124.	At 18·9 mm.: 6·5 (0·34), 5·8 (0·30), c.7·0 (0·37). Adult size c.21 mm., 10 ribs per half whorl at 19·7 mm. diameter.
C. 52590.	At 27·5 mm.: 9·0 (0·32), 8·0 (0·29), 11·9 (0·43). At 21·0 mm.: 7·4 (0·35), 6·7 (0·32), 8·3 (0·39). Adult size c.37 mm., 22 ribs per whorl at 18·4 mm. diameter, 23 at 23·7 mm., 23 at 29 mm.

C. 52591. At 18·2 mm.: 6·2 (0·34), 6·0 (0·33), 7·6 (0·42).
Adult size c.20 mm., 23 ribs per whorl at 18·8 mm. diameter.

C. 52592. At 30·4 mm.: 10·7 (0·35), 9·3 (0·30), 12·7 (0·42).
At 18·9 mm.: 7·3 (0·38), 6·6 (0·35), 7·0 (0·37).
Adult size c.37 mm., 26 ribs per whorl at 21 mm. diameter.

DIAGNOSIS. Coiling less evolute than in other species of *Neokentroceras*. Whorls compressed with rounded quadrangular section. Ornament consists of small pointed umbilical tubercles and falcoid ribs which are wide and flattened at the ventro-lateral angle and swing forwards on the venter. The ribs are roughly associated in pairs with the umbilical tubercles, but in most cases connections between ribs and tubercles are very vague. There are no ventro-lateral tubercles. Keel of moderate size, fading on the last part of the adult body chamber, where the ribs are continuous across the venter as chevrons.

REMARKS. Spath's illustrations of the holotype and one of the paratypes of this species were so poor that Haas (1942: 58–61) was quite unable to interpret the species correctly. The specimens he figured as typical forms of the species (Haas 1942, figs. 6*j*, *k*, pl. 8, figs. 8, 9, pl. 9, fig. 8) are small fragments which are difficult to place, but they have very large tubercles and are probably rather coarsely tuberculate specimens of *N. curvicornu*, while the specimens he figured (Haas 1942, figs. 6*l*, *m*, pl. 8, figs. 10–13, pl. 9, fig. 9) as *N. pseudovaricosum* var. *gracilis* are examples of either *N. curvicornu* or *N. singulare*. However, his figured specimens of *N. costatum* var. *tenuis* Haas (1942: 53, figs. 6*e*, *f*, pl. 7, fig. 26, 27, pl. 8, fig. 1) appear to be genuine specimens of *N. pseudovaricosum*.

The distinguishing character of *N. pseudovaricosum* is the type of ornament at the ventro-lateral edge. Commencing indistinctly at small sharp umbilical tubercles, the ribs rapidly strengthen and are falcoid on the side of the whorl, then they become broad and flattened at the ventro-lateral edge and curve strongly forwards on the venter. True tubercles are not formed at the ventro-lateral edge.

The 7 specimens referred to this species are characterized by these distinctive ribs and are clearly marked off from all other species of *Neokentroceras*. In other characters, however, there is wide variation, as can be seen from the dimensions listed above. C. 20124 and C. 52591 (Pl. 3, figs. 8, 10) are nearly complete adult specimens with the mouth border only just missing in each case; the diameters when complete would have been 21 and 20 mm. respectively. C. 52592 (Pl. 3, fig. 11) is a much larger adult with part of the mouth border preserved at 37 mm. diameter, while C. 52590 (Pl. 3, fig. 9) has final approximated suture-lines at 25·5 mm. diameter followed by a quarter of a whorl of body chamber, indicating a size when complete of about 37 mm. diameter. Rib density varies between 20 and 26 ribs per whorl at 18–22 mm. diameter. C. 52590 has 11 umbilical tubercles and 23 ribs at 29 mm. diameter. Whorl breadth ranges from 30 to 35% of the diameter at 16–21 mm. diameter. The low whorl breadth of 30% in C. 20124 led Spath to the proposal of var. *compressa* for this specimen. It can be seen, however, that the difference in whorl breadth between this specimen and the holotype of the species at the same diameter is only 0·2 mm. or 1%, which is a negligible difference and is much less than the range of variation in the species. Of the three whorl sections figured by Spath (1922: 141, figs. D4, 5*a*, 6), his fig. D4 is accurate, fig. D 5*a* is drawn much too wide, for in this specimen the whorl breadth is always less than the height, while fig. D6 is drawn much too compressed, for the whorl breadth should be 5·8 mm. The earlier part of the whorl in the latter specimen is slightly crushed by compression, and it was probably this that led Spath to the proposal of the name var. *compressa*. It is not advisable to use any varietal names for this species until the full variation is better known, for it is unlikely to be completely expressed in a collection of only 7 specimens.

The degree of variation of adult size in this species is comparable with that found in much larger collections of other small species. The modifications of the ribs just before the mouth border in the smallest and largest adults (C. 52591 and 52592) are very similar. In both cases the last 3 or 4 ribs lose much of the broadening and flattening at the ventro-lateral edge and curve strongly forwards on the venter to join from opposite sides, while the keel almost disappears.

Neokentroceras crassicostatum sp. nov.

Plate 2, fig. 16, Pl. 3, figs. 12–15

1922 *Neokentroceras* sp., Spath: 143, figs. D 7, 7*a*.

HOLOTYPE. C. 52593 (Pl. 3, fig. 12) from Praia do Jombo.

MATERIAL. In addition to the holotype, 7 specimens (paratypes); C. 20126 from the shore at landing place near Hanha, and C. 52594–96, C. 52598–600 from Praia do Jombo.

Dimensions:

C. 52593. At 32 mm.: 9·8 (0·30), 9·4 (0·29), 16·0 (0·50).
22 ribs and 12 umbilical tubercles at 34 mm. diameter.

C. 52600. At 23·6 mm.: 8·3 (0·35), 7·7 (0·32), —.

DIAGNOSIS. Allied to *N. pseudovaricosum*, but more evolute, has larger and more widely spaced ribs clearly connected to umbilical tubercles, and small sharp ventro-lateral tubercles surmounting ribs on inner whorls. Intercalated ribs not connected with tubercles also occur.

REMARKS. Of the eight specimens referred to this species, five have adult body chambers. The holotype (Pl. 3, fig. 12) has final approximated suture-lines at 26 mm. diameter followed by three-eighths of a whorl of body chamber and would have been about 40 mm. diameter at the adult mouth border. C. 52596 (Pl. 3, fig. 14) has nearly half a whorl of body chamber but the final septa are missing; the last 3 or 4 ribs before the aperture curve forwards on the venter and meet from opposite sides, indicating near proximity to the adult mouth border which would have occurred at

37 mm. diameter. C. 52599 (Pl. 3, fig. 13) is a much smaller adult, having approximated suture-lines at 17·5 mm. diameter, half a whorl of body chamber, similar modification of the last 4 or 5 ribs, and the adult mouth border would have occurred at about 25 mm. diameter. C. 52598 (Pl. 3, fig. 15) consists of one-third of a whorl, half septate, half body chamber; the final two suture-lines are only slightly approximated, but the body chamber has the bold widely spaced ribs characteristic of this part of the adult. C. 52600 (Pl. 2, fig. 16) has approximated suture-lines at 19 mm. diameter and nearly half a whorl of body chamber. The other three specimens are fragments, and one of them (C. 20126) was described briefly by Spath (1922: 143).

The small ventro-lateral tubercles on the inner whorls are seen well on the holotype where they occur on the septate whorls up to about 24 mm. diameter. On other specimens they disappear at a smaller size, probably corresponding to about half a whorl before the beginning of the adult body chamber. On the holotype there are 22 ribs and 12 umbilical tubercles per whorl at 34 mm. diameter, and C. 52600 has 21 ribs per whorl at 25 mm. diameter.

The ribs in this species are similar in form to those in *N. pseudovaricosum*, but they differ in being stronger and more widely spaced and show distinct connections with the umbilical tubercles. Occasional ribs are intercalated and commence at about the middle of the side of the whorl and are not connected with the umbilical tubercles. Distinct ventro-lateral tubercles on the inner whorls also serve to distinguish this species from *N. pseudovaricosum*. The species shows considerable resemblance in side view to *Hysteroceras varicosum* var. *angolana* (Haas 1942, pl. 1, fig. 21, pl. 2, fig. 1). In the latter variety, however, the ribs are bold and continuous across the venter of the whole of the body chamber, while the keel and small ventro-lateral tubercles of the septate whorls are lost at about the beginning of the body chamber. In *N. crassicostatum* the keel is present on the whole of the body chamber and only the last 3 or 4 ribs are continuous across the venter in the form of V-shaped chevrons.

Family **PHYLLOCERATIDAE** Zittel 1884

Genus ***NEOPHYLLOCERAS*** Shimizu 1934

Neophylloceras ultimum Spath

1953 *Neophylloceras ultimum* Spath: 4, 49, pl. 7, fig. 7.

Holotype. C. 41477, the only specimen, from Barra do Dande.

Remarks. Several comparable species of *Neophylloceras* have been described since Spath (1953: 4, pl. 7, figs. 7*a*, *b*) named and figured this single Angolan specimen. Its greatly subdivided and complex suture-line shows through the very thin transparent shell, but the continuity is not sufficient to allow it to be figured. The extremely fine and closely spaced striae can be seen clearly on Spath's figures and this character serves to distinguish *N. ultimum* from all other species. In fact 32 striae cross a length of 10 mm. of venter immediately preceding the aperture of this specimen, and this density is nearly twice that of the nearest comparable species at a similar size. Such comparable forms are *N. ramosum* (Meek) which ranges from the Turonian to the Upper Campanian and probably the Lower Maastrichtian in western north America and Japan (Matsumoto 1959*b*: 1–5, pl. 1, fig. 1), *N. hetonaiense* (Matsumoto 1959*b*: 5) in the Campanian and Maastrichtian of western North America, Japan and Graham Land, *N. lambertense* Usher (1952: 50, pl. 1, figs. 1–3) in the Upper Campanian and Lower Maastrichtian of British Columbia, and *N. nera* (Forbes) from the Campanian or Maastrichtain in southern India (Kossmat 1895: 166, pl. 16, fig. 2). *N. ramosum* and *N. hetonaiense* have recently been figured from Upper Campanian or Lower Maastrichtian beds in Alaska (Jones 1963: 22, pl. 6, pl. 7, figs. 1–5) and one of the specimens (pl. 6, figs. 2, 4–6) of the former species has extremely fine striae almost comparable with those of *N. ultimum*.

The position of the genus *Neophylloceras* and its relationship with its Lower Cretaceous ancestor *Hypophylloceras* have been discussed by Matsumoto (1959*a*: 55–58). Other phylloceratid species in the Campanian and Maastrichtain belong mainly to the genus *Epiphylloceras* Collignon 1956. The type species, *E. surya* (Forbes), occurs in Angola (Haughton 1925: 268, pl. 12, figs. 3–5) and southern India (Kossmat 1895: 158, pl. 16, fig. 1) and is characterized by bundled ribbing, one rib of each bundle being usually enlarged. Several other species occur in the Maastrichtian of Madagascar (Collignon 1956: 24–25).

Family **TETRAGONITIDAE** Hyatt 1900

Subfamily **GAUDRYCERATINAE** Spath 1927

Genus ***ANAGAUDRYCERAS*** Shimizu 1934

TYPE SPECIES. *Ammonites sacya* Forbes 1846.

The interpretation and characteristics of this genus have been discussed at length by Wright & Matsumoto (1954: 111–113) and Matsumoto (1959: 73; 1959*a*: 138). Wiedmann's (1962: 156–158) relegation of *Anagaudryceras* to the synonymy of *Gaudryceras* is not accepted. The ornament of all but the adult stage of *Anagaudryceras* is so fine that the shell appears to be smooth, while *Gaudryceras* is characteristically covered with fine ribs. This difference is sufficient for generic distinction in keeping with the scale of differences usually adopted for Cretaceous genera (e.g. by Wright 1957; Matsumoto 1959, 1959*a*, 1959*b*). The only additional point concerning the morphology of *Anagaudryceras* which can usefully be made here concerns the suture-line. Spath determined the species described below as an evolute species of *Pseudophyllites*. When one of the suture-lines was etched out, however, it proved to have quadrifid lateral saddles (basically bifid, with each arm divided again) and a single large saddle in the internal suture-line. In *Pseudophyllites* the lateral saddles are basically trifid and there are two or more saddles in the internal suture-line. These differences in the suture-lines enable involute species of *Anagaudryceras* to be distinguished from evolute species of *Pseudophyllites* where there are few or no other differences.

Species of *Anagaudryceras* range from the Upper Albian to the Maastrichtian and have a world-wide distribution: examples have been described from Europe, North Africa, Angola, Madagascar, India, Japan, Alaska, California, New Zealand and Antarctica. The wide distribution has led to a multiplicity of specific names, but none of the faunas contains more than a very few specimens and it is not yet possible to make an assessment of the variation within a species. The 17 available specific names are probably far too many (listed in Collignon 1956: 66, 68–70). One of the main species is *A. sacya* (Forbes; see Matsumoto 1959: 72) which has broad band-like ribs on the body chamber and well marked constrictions on earlier whorls. It ranges from the Upper Albian to the Turonian and possibly higher; *A. buddha* (Forbes), *A. revelatum* (Stoliczka) and *A. limatum* (Yabe) are synonyms; Yabe's variety *obscura* is probably a true variety, but larger and more complete specimens of the New Zealand Campanian species *A. subsacya* (Marshall) and *A. crenatum* (Marshall) are required before it can be determined whether they also are synonyms. The second main species has only weak constrictions and no band ribs on the body chamber. In the Maastrichtian this is *A. mikobokense* Collignon and *A. aureum* (Anderson) is clearly a synonym; in India Cenomanian ammonites of very similar morphology have the three specific names *A. involutum* (Stoliczka), *A. madraspatanum* (Stoliczka) and *A. utaturense* Shimizu, and in Japan *A. yamashitai* (Yabe) has only a marginally smaller umbilicus, but is Santonian. This leaves *A. politissimum* (Kossmat) from the Turonian to Santonian of India which has a smaller whorl height and whorl breadth at the same diameter as *A. mikobokense* and may represent a different species, and *A. subtililineatum* (Kossmat) from the Campanian or Maastrichtian of India which is too fragmentary for identification. Both *A. multiplexus* (Stoliczka) from the Cenomanian of India and *A. coalingense* (Anderson) from the Maastrichtian of California represent an evolute many-whorled species, with constrictions but no known ribs; much larger collections are needed to determine whether these are conspecific.

Such a specific classification could be expected to emerge from a comparison of abundant material of *Anagaudryceras* if it were available. The collection described below consists, however, of only 13 specimens, yet this is one of the largest collections of a single species of the genus found so far.

Anagaudryceras mikobokense Collignon

Plate 4, figs. 1–3; Text-fig. 1

1938 *Gaudryceras politissimum* Kossmat; Collignon: 92, pl. 7, fig. 2.
1952 *Gaudryceras aenigma* Haas: 11, figs. 18-20.
1956 *Anagaudryceras mikobokense* Collignon: 59, pl. 8, fig. 1.
1958 *Lytoceras* (*Gaudryceras*) *aureum* Anderson: 184, pl. 71, fig. 1.
1959*a* *Anagaudryceras mikobokense* Collignon; Matsumoto: 139, pl. 38, fig. 1.

MATERIAL. 13 specimens, C. 52636–48, from 1 km. north of Egito, Angola.

DESCRIPTION. The innermost whorls are exposed and evolute, while the degree of involution increases slightly with increasing size. The whorl height and breadth are equal at about 34 mm. diameter; at smaller sizes the breadth exceeds the height; at larger sizes the height progressively exceeds the breadth, and at 80 mm. diameter the breadth/height ratio has a range of 0·80 to 0·90. The largest specimen is wholly septate at its maximum diameter of 85 mm., and none shows any adult characters. The shell is smooth and unornamented up to about 30 mm. diameter; at larger sizes there are straight radial growth striae on well preserved parts of the shell, and irregularly developed low, widely spaced radial ribs which tend to increase in strength with increase in size. These ribs are inclined forwards at the umbilical margin, curve slightly backwards on the side of the whorl and become radial in crossing the venter. There are no constrictions, although where the ribs cross the venter they often have the appearance of a low flare, of the sort that are sometimes associated with constrictions. In the suture-line there are four equal-sized folioles terminating each of the first and second lateral saddles and the first auxiliary saddle, then there are two smaller auxiliary saddles before the umbilical edge and a single large lateral saddle in the internal suture-line. There are small upright saddles in the middle of the first lateral and first auxiliary lobes. At large sizes the suture-lines become somewhat further subdivided.

Remarks. These are the specimens originally identified as "*Pseudophyllites* sp. nov. (a more evolute form than *P. indra* Forbes sp.)" by Spath (1940*a*: 52; 1951: 8; 1953: 49). They are now referred to *Anagaudryceras* rather than to *Pseudophyllites* because of their suture-line characters, which, as described above, enable the two genera to be separated. Two specimens of average characters are figured in Pl. 4, figs. 1, 3, a slightly more involute specimen is figured in Pl. 4, fig. 2, and a complete suture-line is shown in Text-fig. 1.

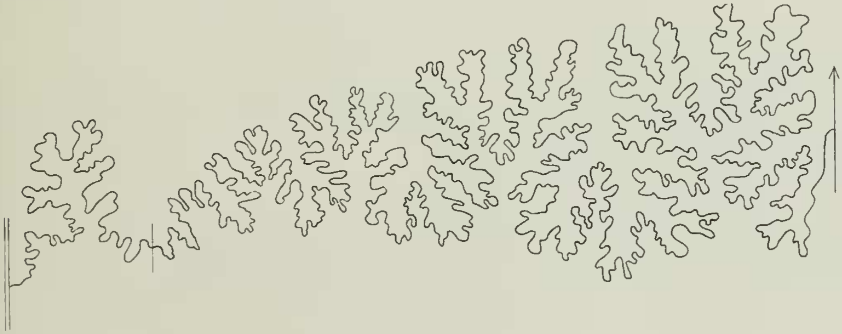


Fig. 1. Complete suture-line of *Anagaudryceras mikobokense* Collignon from venter to dorsum at whorl height of 28 mm. C. 52646, from Upper Campanian, 1 km. north of Egito, Angola. ×2·6.

Variation among the 13 specimens is not large and is mainly in the whorl proportions. Graphs of whorl height and umbilical width plotted against the diameter show a range in whorl height of 28·3 mm. to 32 mm. at 70 mm. diameter, and in umbilical width of 22 mm. to 24 mm. at the same size. Whorl breadth is more constant, the greatest variation being less than 2 mm. at any diameter between 40 mm. (15·5 mm. whorl breadth) and 80 mm. (29·5 mm. whorl breadth). All the specimens have the very reduced ornament on the outer surface of the shell, and this is even more reduced on the inner surface.

An example of the present species from Egito was described and figured by Haas (1952: 11, figs. 18–20) as *Gaudryceras aenigma* Haas. This specimen is a perfect match for the one figured here in Pl. 4, fig. 3. The true *G. aenigma* (Haas, 1942: 167, pl. 42, fig. 3, pl. 44, fig. 2) is an Albian species and has the fine sharp ribs characteristic of *Gaudryceras*.

The Angolan specimens compare very closely with the holotype from the Lower Maastrichtian of Madagascar described by Collignon. That holotype differs only in the possession of very faint, rare constrictions. The Californian specimens described by Anderson and by Matsumoto are also very similar to the Angolan specimens and undoubtedly conspecific. Both Collignon (1956: 59) and Matsumoto (1959*a*: 139) have included the two specimens from the Campanian of Antarctica figured by Kilian & Reboul (1909: 14, pl. 1, figs. 7, 8) in the synonymy of *A. mikobokense*. Although these Antarctic specimens appear to be smooth, one (fig. 7) shows what appears to be a strongly curved constriction, and both show traces of strongly prorsiradiate fine ribs. They are probably specimens of *Gaudryceras* with the ribs worn away, as is undoubtedly the case in the two further Antarctic specimens figured by Kilian & Reboul (1909, pl. 1, fig. 6) and Spath (1953: 12, pl. 1, fig. 10).

Other specimens of similar morphology to *A. mikobokense* but of different ages have already been briefly mentioned above, but in view of the small number of specimens involved and the difficulties of comparison, further discussion would not be of value.

Genus ***GAUDRYCERAS*** Grossouvre 1894

TYPE SPECIES. *Ammonites mitis* Hauer 1866.

The characteristics and synonymy of this genus have been discussed by Wright & Matsumoto (1954: 111–113) and Matsumoto (1959*a*: 141), who concluded that subdivision of the genus is not necessary.

The specific nomenclature of *Gaudryceras* is in an even greater state of confusion than that of *Anagaudryceras* discussed above. Species of *Gaudryceras* have a world-wide distribution similar to that of *Anagaudryceras*, and also include examples known from South-East Africa, British Columbia and South America. About 27 specific names have been proposed (for lists see Collignon 1956: 67–69), plus *G. alamedense* (Smith 1898), *G. devallense* Anderson 1958, *G. filicinctum* (Whiteaves 1876), *G. navarrense* Wiedmann 1962, *G. sachalinense* (Schmidt 1873) and *G. vascogoticum* (Wiedmann 1962). The number of known specimens of *Gaudryceras* is much greater than in the case of *Anagaudryceras*, and from the rich faunas in Madagascar and Japan it should be possible to work out the variation within each species and a good specific classification. It has been pointed out by Yabe (1903: 14) and Collignon (1956: 48–49) that at about 100 mm. diameter the whorls of many species become rapidly more massive, with whorl height and breadth increasing markedly and umbilical size decreasing markedly. Outer and inner whorls of the same species often look very different, therefore, and many have been given different specific names.

Interpretation of the type species, *G. mite*, is difficult, because the holotype figured by Hauer (1866: 305, pl. 2, figs. 3, 4) is distorted to an elliptical shape, and the low whorl breadth may also be due to crushing. Grossouvre (1893: 227, pl. 26, fig. 4, pl. 27) figured another small specimen and also a much larger specimen which is a good example of the much more massive appearance of the whorls at large sizes. This species retains fine ribs up to the largest known sizes, but further study of the holotype and of a topotype collection is necessary before it can be properly defined.

Gaudryceras varagurense Kossmat

Plate 4, fig. 5; Pl. 5, figs. 1, 2.

1895 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat: 122, pl. 17, fig. 9, pl. 18, figs. 2*a–c*.
?1909 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat; Kilian & Reboul: 12, pl. 1, fig. 6.
?1929 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat; Barrabé: 180, pl. 9, fig. 16.
?1930 *Gaudryceras varagurense* Kossmat; Besairie: 569, pl. 21, fig. 4.
1931 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat; Basse: 14, pl. 1, figs. 25, 26.
1931 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat; Collignon: 11, pl. 1, figs. 5, 6, pl. 8, fig. 2.
1952 *Puzosia lytoceroides* Haas: 8, figs. 14–17.
1953 *Gaudryceras* (*Neogaudryceras*) *pictum* (Yabe); Spath: 12, pl. 1, fig. 10.
1956 *Gaudryceras varagurense* Kossmat; Collignon: 56, pl. 5, fig. 6.
1962 *Gaudryceras navarrense* Wiedmann: 158, pl. 9, fig. 3.

MATERIAL. 11 specimens, C. 52649–59, from 1 km. north of Egito, Angola.

DESCRIPTION. The whorls are evolute and the umbilicus shallow. The whorl section is rounded with greatest breadth at or near the umbilical edge. Whorl height and breadth are equal at about 40 mm. diameter; at smaller sizes breadth exceeds height, at larger sizes height exceeds breadth. The ornament consists of fine ribs, some of which bifurcate on the side of the whorl near the umbilical edge; there are also single ribs which do not divide, and a few intercalated ribs that do not reach the umbilical edge. The ribs are inclined strongly forwards on the umbilical walls, bend slightly backwards on the side of the whorl, then bend forwards again on the venter. There are 6 to 8 constrictions per whorl which follow the line of the ribs exactly, and appear as constrictions on the internal cast with a ridge or collar behind, whilst on the shell they appear as thickened ribs only.

REMARKS. Spath (1951: 8) determined these specimens as "*Gaudryceras* sp. (*varagurense*, auct, *non* Kossmat)". Haas (1952: 8, figs. 14–17) had two examples of this species from Egito amongst his collection. He figured one of them and made it the holotype of a new species, *Puzosia lytoceroides*, but it is clearly a fine example of *Gaudryceras varagurense* and compares very closely with the specimen figured here in Pl. 5, fig. 1.

The largest specimen in the present collection is 85 mm. diameter, and does not show the massive whorls which the species develops at about 100 mm. diameter. Measurements of the whorl proportions obtained from 6 specimens were inadequate for an assessment of the variation of the species, but they were plotted graphically and could be compared with the proportions of other specimens. The fine ribs continue up to the aperture of the largest individual, and from a comparison with the type specimens of species which develop coarser ribbing, it is deduced that the present collection belongs to a species which retains fine ribbing throughout growth. Such species with coarse ribs are known especially from Japan (e.g. *G. densiplicatum* (Jimbo)) and all of them show the coarse ribbing well before the growth stage reached by the Angolan specimens. In another more closely related species, or group of species, the inner whorls are indistinguishable from those of the Angolan specimens, but at 50 to 70 mm. diameter the ribs, while remaining small, become more widely spaced. This is known in western north America as *G. demanense* (Whiteaves) (Usher 1952: 59, pl. 4, fig. 1), in Japan as *G. tenuiliratum* (Yabe 1903: 19) and in Madagascar as *G. lauteli* Collignon (1956: 57, pl. 7, fig. 1), all of which are either conspecific or closely related.

For the fine ribbed species to which the Angolan specimens belong the oldest name is *G. varagurense* (Kossmat 1895), for the difficulties of interpretation outlined above make it inadvisable to use *G. mite* (Hauer 1866) until it can be properly defined. The holotype from the Santonian of southern India is a broken and incomplete specimen, but its ornament seen on several whorls up to 100 mm. diameter, and its dimensions obtained from a reconstruction of the spiral, compare closely with those of the Angolan specimens. Other species which are very close to or conspecific with *G. varagurense* are: *G. analabense* Collignon (1956: 54, pl. 6, fig. 3) and *G. beantalyense* Collignon (1956: 53, pl. 5, fig. 3) both from the Coniacian of Madagascar, and *G. variocostatum* van Hoepen (1921: 7, pl. 2, figs. 10–12) from the Santonian of Pondoland, which is based on a specimen of only 40 mm. diameter. *G. cinctum* Spath (1921: 41; 1922*a*: 118, pl. 9, fig. 3) from the Santonian of Natal appears to be more involute, but it is too small for proper comparisons. The Japanese Santonian to Maastrichtian species *G. striatum* (Jimbo 1894: 35, pl. 6, fig. 6) and its variety *G. striatum* var. *pictum* Yabe (1903: 33, pl. 4, fig. 6) are also fine ribbed, but again the material is too small and poorly known. *G. navarrense* Wiedmann (1962: 158, pl. 9, fig. 3) from the Campanian of northern Spain appears to be a typical *G. varagurense* showing all the normal characters. *G. propemite* Marshall (1926: 142, pl. 28, figs. 3, 4) from New Zealand and *G. delvallense* (Anderson 1958: 183, pl. 41, fig. 4) from California have strongly curved and wiry ribs and probably represent a different species. Any attempt to sort out the synonymies outlined here must await the description of the rich Japanese faunas and a re-assessment of the Madagascan specimens in the light of the results.

Family **BACULITIDAE** Meek 1876

Genus ***BACULITES*** Lamarck 1799

TYPE SPECIES: *B. vertebralis* Lamarck (1801: 103) by subsequent designation by Meek (1876: 391).

Baculites vertebralis was introduced by Lamarck without any description, but with references to figures of Faujas (1799: 141, pl. 21, figs. 2, 3) and Bourguet (1742, pl. 49, figs. 313–316). Although the figures of these two authors showing short smooth septate fragments are very poor, it can at least be seen that the whorl sections of all of them are circular or elliptical. In a later work Lamarck (1822: 647) discarded the specific name *vertebralis* in favour of *B. faujasii* which he proposed for the same species, with a short description now added, a reference to the figure of Faujas only, and a statement that the type specimen (in his collection) came from the mountain of Saint-Pierre, near Maastricht (in south Limbourg, Holland). This type specimen is lost. J. de C. Sowerby (1828; 186, pl. 592, fig. 1) was able to interpret *B. "faujasii"* correctly from this description, stating that the venter and dorsum were equally rounded, the whorl section elliptical and the shell smooth. Topotypes from St. Pierre, Limbourg, were well figured by Binckhorst (1861: 40, pl. 5*d*, figs. 1*a*-*h*). This interpretation of *B. vertebralis* as a smooth species with an elliptical whorl section and of Maastrichtian age is now well established (e.g. Nowak 1908: 346, fig. 8*a*, pl. 14, fig. 8).

The second important early species of *Baculites* is *B. anceps* Lamarck, 1822. Its interpretation will have to be discussed at length because the Angolan specimens are very close to a form from the Pacific region which has been referred to a subspecies of *B. anceps*. The type area for *B. anceps* is the outcrops of the Calcaire à *Baculites*, in Manche, France. *B. anceps* shows considerable variation, and as *B. vertebralis* occurs in the same beds, it is important to establish the identification of the latter species, so that its clear separation from *B. anceps* can be demonstrated. The necessity for designating a type specimen for *B. anceps* and describing the characters of the type population has been stressed by Matsumoto (1959*a*: 130–136) and Matsumoto & Obata (1963: 59–63), for until this is done no further progress can be made in describing similar species from other parts of the world. Application will be made to the ICZN to have the specimen designated below as neotype officially recognized.

Baculites anceps Lamarck

Plate 4, fig. 4; Pl. 5, figs. 4, 5; Pl. 6, figs. 1–5; Text-figs. 2, 3, 5–12

1816 *Baculites vertebralis* Lamarck; Defrance: supplement p. 60, pl. 22, figs. 1–3 (date of plate uncertain).
1822 *Baculites anceps* Lamarck: 648.
1825 *Baculites vertebralis* Lamarck; Blainville: 380, pl. 12, figs. 1–3.
1831 *Baculites anceps* Lamarck; Deshayes: 224, pl. 6, fig. 2.
1837 *Baculites anceps* Lamarck; Bronn: 732, pl. 33, fig. 6.
1842 *Baculites anceps* Lamarck; d'Orbigny: 565, pl. 139, figs. 1–7.
1876 *Baculites anceps* Lamarck; Schlüter: 145, pl. 40, figs. 2, 6.
1888 *Baculites anceps* Lamarck; Prestwich: pl. 12, fig. 16.
1889 *Baculites anceps* Lamarck; Griepenkerl: 106, pl. 11, fig. 2.
?1891 *Baculites valognensis* Böhm: 50, pl. 1, fig. 13.
1908 *Baculites anceps* Lamarck var. *valognensis* Böhm; Nowak: 335, figs. 1–4 (p.331), figs. 6, 7, 9, 12 (p.337); pl. 14, figs. 6, 7.

NEOTYPE. BM(NH) 32573, from the "Calcaire à *Baculites*" of Manche, France, is here designated as neotype. It was originally part of Mantell's collection.

DIAGNOSIS. A species of *Baculites* in which the venter is always sharpened, and sometimes a keel is differentiated by slight grooves on either side. The dominant form is smooth at all growth stages and unconstricted, but others occur in which ribs varying between weak and strong are formed on either body chamber or septate portion. These ribs are large and arcuate on the dorsal half of the shell, then they swing well forwards and are reduced almost to striae that are straight up to the keel where they form slight crenulations in some cases. Fine striae occur between the main ribs on the external surface of the shell. A minority of specimens have constrictions, which occur indiscriminantly on smooth or ribbed forms and vary in strength between weak and well marked.

DESCRIPTION. The type population occurs in the Calcaire à *Baculites* in Manche, Normandy. The locality from which most specimens have been obtained is Valognes. The largest collection is that in the British Museum (Natural History) and consists of 84 specimens, 47 of them obtained by Sowerby from de Gerville. The following description is based on this collection, plus two of d'Orbigny's originals and four specimens from de Vibrayes' collection in the Muséum national d'histoire naturelle, Paris, sent by Dr. J. Sornay, a total of 90 specimens.

The largest specimen is a body chamber fragment with the mouth border missing, and has a cross section height of 32 mm. and a width of 22 mm. at the broken aperture. The height of the shell at the final suture-line before the body chamber varies between 14 and 26 mm., but some of the smaller specimens are probably immature. Only one specimen (Pl. 5, fig. 4) has characters which in a spirally coiled ammonite would be taken as indicative of an adult: its mouth border is flared and the final two suture-lines are much closer together than any of the preceding ones; it is a small specimen compared with many of the others, the shell height at the mouth border and final suture-line being 16 and 14·5 mm. respectively. Such flared mouth borders are seen in a number of specimens, and they all have a long rostrum on the venter and a smaller one on the dorsum, as shown in one of the specimens figured by d'Orbigny (1842, pl. 139, figs. 3–5). In all specimens the cross section is sharpened or keeled on the venter, broad and slightly flattened on the dorsum, and has well rounded sides, so that even though the venter and dorsum are markedly different the thickest part of the shell is close to the mid-point of the side. Shallow grooves defining a distinct keel are present in a few specimens.

The ornament shows considerable variation. The two variables are the presence or absence of ribs and constrictions, and the following table shows the number of specimens belonging to each of the nine possible combinations in the collection of 90 specimens.

Although there are no clear divisions between the groups, such a grouping expresses the variation, and shows that 59 of the 90 specimens are smooth, 16 have weak ribs and 15 strong ribs; in each of these three groups between one-third and one-quarter of the specimens have constrictions. The largest group, 42 smooth and unconstricted specimens, accounts for nearly half the collection. The ribs are highly arcuate and strongly developed just dorsal of the middle of the side; they are inclined strongly forwards, straight and reduced to striae on the ventral half of the side, and reach the venter to form slight crenulations on the keel in some cases; they are also straight on the dorsum over which they pass without interruption, but are inclined less strongly forwards. The constrictions are similar to the ribs on the dorsal half of the side, but on the ventral half they at first follow the ribs, then bend slightly backwards before swinging well forwards again to reach the venter.

		Constrictions			
		Absent	Weak	Strong	
RIBS	Absent	42	4	13	59
	Weak	11	3	2	16
	Strong	11	0	4	15
		64	7	19	90

The specimens figured here to show the range of morphology are: the neotype (Pl. 5, fig. 5) which has a smooth body chamber, very weak ribs on the septate part and no constrictions; a smooth, unconstricted specimen, showing the final two suture-lines close together and part of the flared mouth border (Pl. 5, fig. 4); a specimen with ribs of moderate strength (Pl. 6, fig. 1); a fragment with strong ribs (Pl. 4, fig. 4); two smooth specimens with constrictions (Pl. 6, figs. 2, 5); and two ribbed specimens with constrictions (Pl. 6, figs. 3, 4).

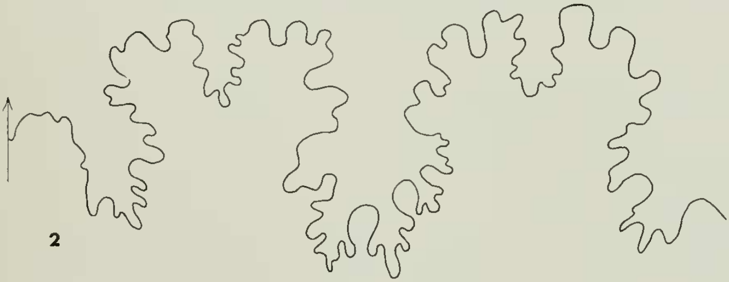
REMARKS. Matsumoto (1959*a*: 130, Matsumoto & Obata 1963: 59) has already stated that the interpretation of *Baculites anceps* must be stabilized by the designation of a type specimen, and has suggested (quoting Wright *in litt.*) that such an interpretation should be based on d'Orbigny's (1842) figures of the species. An examination of the original description and the type population of the species leads to somewhat different conclusions.

Lamarck (1822: 648) described the species as follows:

> "Baculite gladiée. *Baculites anceps*.
>
> *B.* testâ rectâ, compressiusculâ, ancipiti, laevi; uno latere subacuto, altero crassiore, obtuso; siphone marginale ad latus acutum. Habite . . . Fossile d'Angleterre. Mon cabinet. Elle atteint jusqu'à 13 pouces de longueur."

Lamarck's original specimens are lost, but from this description it is clear that this is a smooth species of *Baculites* with a subacute venter and a flat dorsum. It is most unlikely that Lamarck's specimens came from England where the species is still not known to occur, and from interpretations of the species shortly after Lamarck it is much more likely that his originals came from the Calcaire à *Baculites* in Manche, Normandy. Specimens probably from Manche were described by Defrance (1816: 160, pl. 22, figs. 1–3) and Blainville (1825: 380, pl. 12, figs. 1–3) under the name *B. vertebralis*; in both descriptions it is clear that the species referred to is *B. anceps*, and the figured specimen appears to be entirely smooth. Further specimens from Manche, collected by de Gerville at Valognes, were described by Deshayes (1831), this time under the correct name *B. anceps*; the figured specimen is a short smooth fragment, said to be keeled. The best interpretation of *B. anceps* prior to d'Orbigny is that of Bronn (1837), who figured a fine specimen from Manche, that is 265 mm. long, keeled, with a smooth septate portion and fine ribs on the body chamber; this was certainly sufficient to fix the identity of the species. The Swedish specimen figured as *B. anceps* by Hisinger (1837: 31, pl. 6, fig. 2) has a cross section that is close to a perfect ellipse and does not belong to this species. In view of the establishment of *B. anceps* as a mainly smooth species, it is surprising that d'Orbigny (1842) chose as his figured specimens two Manche examples that had large ribs on their body chambers. D'Orbigny was well aware of the variation of the species between such ribbed forms and entirely smooth forms, and his was the first good description of this variation. He also stated that the species was known only from Manche, even though he included (wrongly) Hisinger's Swedish specimen in his synonymy. Authors following d'Orbigny added little to his interpretation of *B. anceps*. Binckhorst (1861: 42, pl. 5*d*, fig. 3) referred a specimen to this species which is, in fact, a *Eubaculites* with a tabulate venter from the Maastrichtian of Limbourg. Schlüter (1876) and Griepenkerl (1889) recorded the species from Germany. Griepenkerl followed d'Orbigny in considering the variety with large ribs as the normal form, and he proposed the name var. *sublaevis* for the smooth form, a name that is not necessary because the smooth form is the dominant form in the type population. Although the specimen figured by Prestwich (1888: 332, pl. 12, fig. 16) was labelled "Upper Chalk" and in the absence of a stated locality would be taken for an English specimen, it is from Manche, and the best one figured hitherto; it is 205 mm. long, one half septate with very fine striate ribs, and the other half smooth body chamber. The German specimen figured by Böhm (1891) as *Baculites valognensis* may be an example of *B. anceps*, but it is a small fragment and not really recognizable. Nowak (1908) interpreted Böhm's species as merely a variety of *B. anceps*, and figured two Manche specimens, one with fine ribs on the septate part, the other with somewhat larger ribs on the body chamber. As these are also part of the normal range of variation in the type population (they are not like the really boldly ribbed forms) the varietal name is again unnecessary. Nowak (1908: 328, figs. 1–5 (p.329), pl. 14, figs. 1–5, 10) also proposed a new variety *leopoliensis* for a form from the Cretaceous of Poland that has bold ribs on the body chamber and fine secondaries retained on the venter to a large size. But the whorl section of this form does not show a consistent keel on the venter, which is the most characteristic feature of *B. anceps*, and the variety should be excluded from *B. anceps*. No further descriptions or figures of *B. anceps* have been given.

From the discussion above it is clear that *B. anceps* was interpreted as a smooth or finely ribbed species prior to d'Orbigny, and it is now known that smooth forms are dominant in the type population. The specimen chosen as neotype is therefore an almost smooth example and is not like the coarsely ribbed examples figured by d'Orbigny; it is the specimen, B.M. (N.H.) 32573, originally figured by Prestwich (1888, pl. 12, fig. 16), and was from Mantell's collection, presented to the British Museum (Natural History) with the label "*Baculites anceps*, Normandy". It is typical of the dominant form of the species, having no constrictions, and only very fine ribs on the septate part. Plaster-casts of the two best specimens in d'Orbigny's own collection (no. 7204) were kindly sent to me by Dr. J. Sornay, but neither is good enough to be made the type specimen, nor were they the originals of any of d'Orbigny's figures. Four specimens from de Vibrayes' collection in Paris, also sent on loan by Dr. Sornay, are smaller and less well preserved than the neotype. Amongst the material in the British Museum (Natural History) from which the above description of the type population was drawn, the one designated as neotype is the best specimen for which a definite locality is known (even though this is only "Normandy"). It is slightly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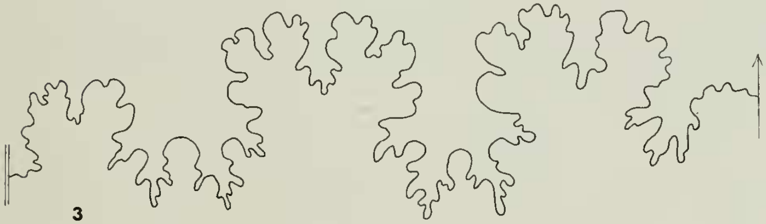
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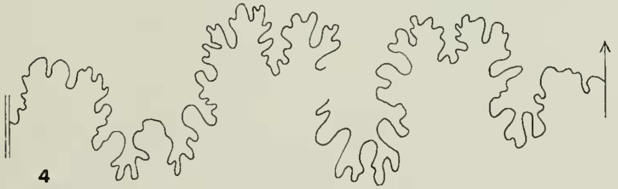
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FIGS. 2–4. Suture-lines of *Baculites*. Fig. 2. *Baculites anceps* Lamarck. Fourth suture-line from body chamber. Neotype, B.M.(N.H.) 32573, from Lower Maastrichtian, Calcaire à *Baculites*, Normandy. ×4·5. Fig. 3. *B. anceps* Lamarck. Suture-line at cross section height of 16 mm. B.M.(N.H.) 6408, same horizon and locality. ×4·8. Fig. 4. *B. subanceps* Haughton. Last suture-line at cross section height of 11·5 mm. C. 52730, from Upper Campanian, Carimba, Angola. ×5.

better preserved and more complete than the best of the 47 Valognes specimens obtained by Sowerby from de Gerville and forming the main part of this collection.

The characteristic feature of *B. anceps* is the keeled or sharpened venter. Variation in other characters is considerable, ranging from completely smooth to boldly ribbed types and including unconstricted and constricted specimens. There is no reason to believe that any of these should be separated specifically, for all intermediates exist, even specimens with very weak constrictions, and all are united by the keeled venter. *B. anceps* is very common at only one horizon in the Calcaire à *Baculites* of Manche (Grossouvre, 1901: 286, the lowest bed), where it has every appearance of forming a normally variable single population. *B. vertebralis* Lamarck, which occurs less commonly in the same bed, has a completely different cross section. The age of this bed is Lower Maastrichtian.

The specimen described and figured by Desmarest (1817: 49, pl. 2, figs. 4–6) as *B. dissimilis* has a whorl section that is close to elliptical with no marked difference between venter and dorsum. The specific name is not a senior synonym of *B. anceps*. The Californian and Japanese specimens described by Matsumoto (1959*a*: 130–136, pl. 34, fig. 3; pl. 35, fig. 1) and Matsumoto & Obata (1963: 59–63, pl. 20, fig. 3) as *B. anceps pacificus* also lack the keel of *B. anceps*, and should be excluded from that species. They belong to *B. subanceps* as described below.

Baculites subanceps Haughton

Plate 5, fig. 3; Pl. 6, figs. 6, 7; Pl. 7, fig. 1; Text-figs. 4, 13–15

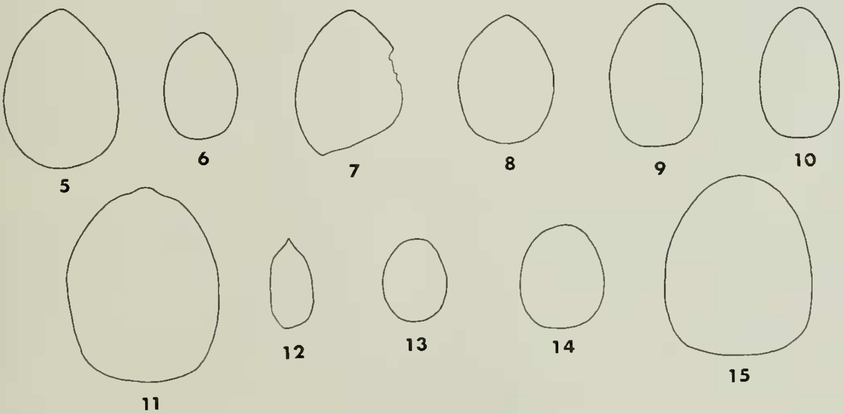
1925 *Baculites subanceps* Haughton: 278, pl. 14, figs. 6–8.
1959*a* *Baculites* aff. *B. anceps* Lamarck; Matsumoto: 130, pl. 34, fig. 3; pl. 35, fig. 1.
1963 *Baculites anceps pacificus* Matsumoto & Obata: 59, pl. 20, fig. 3.

LECTOTYPE. South African Museum No. 6829 (Pl. 6, fig. 6) from Carimba.

MATERIAL. In addition to the lectotype, ten paralectotypes all numbered 6829 in the collection of the South African Museum, Capetown, and four specimens in the British Museum (Natural History) (C. 52729–32). All from Carimba.

DESCRIPTION. The largest specimen (Pl. 7, fig. 1) is a fragment of a body chamber with a short part of the flared mouth border preserved. The height and width of the cross section close to the mouth border are 37 and 30 mm. respectively. This fragment is 120 mm. long and no part of the septate shell is preserved. Its cross section is close to elliptical, but has two wide and shallow grooves on either side of the evenly rounded venter (Pl. 7, fig. 1). The shell is nearly smooth and there is a long ventral rostrum and a short dorsal rostrum at the mouth border. All the other specimens are smaller; some (e.g. Pl. 5, fig. 3) have presumably immature, unflared mouth borders, and the largest final suture-line before a body chamber occurs at a cross section height of 23·5 mm.; the cross section (Text-figs. 13–15) in all of them shows a flattened dorsum, a narrower but well rounded venter, and rounded sides; none has any signs of grooves on either side of the venter. There are no final crowded suture-lines. The ornament is similar to that of the ribbed forms of *B. anceps*; prominent arcuate ribs on the dorsal half of the side are projected strongly forwards and reduced to striae on the ventral half, then (unlike the ribs of *B. anceps*) they increase in strength again and bend slightly back to pass over the rounded venter as prominent crenulations; there are between 2 and 3 times as many such ribs crossing the venter as there are arcuate ribs on the side. The ribs are also reduced to striae across the dorsum and are projected only slightly forwards. All the specimens bear such ribs except the single largest one which is nearly smooth. There are no constrictions.

REMARKS. Haughton (1928: 278) had "numerous examples" of this species and figured three of them. A holotype was not designated, so the whole collection consists of syntypes and a lectotype designation can be made. The original of Haughton's pl. 14, fig. 6 is lost or not available for study, and as this figure does not show any of the ornament it is not suitable to be a lectotype. The specimen from which Haughton obtained the cross section of his pl. 14, fig. 8 (refigured here Pl. 7, fig. 1) is a very large smooth body chamber fragment, with shallow ventral grooves peculiar to its large size, and is also unsuitable for a lectotype. The lectotype designated is therefore the medium-sized specimen figured in Pl. 6, fig. 6, which is half septate, half body chamber, and shows the ornament well. It is one of the best preserved syntypes. Two further specimens are figured (Pl. 5, fig. 3; Pl. 6, fig. 7; Text-figs. 13, 15) which show the ornament and cross section at different sizes. Little variation in the ornament can be detected in the 15 specimens, for all the medium-sized examples are ribbed and the two largest body chambers become nearly smooth. The venter is smoothly rounded in all cases with no trace of sharpening or of a keel.



FIGS. 5–15. Cross sections of specimens of *Baculites* figured in the plates. For details of individual specimens see plate explanations indicated below. Figs. 5–12. *Baculites anceps* Lamarck. Fig. 5 = Pl. 4, fig. 4; Fig. 6 = Pl. 5, fig. 4; Fig. 7 = Pl. 5, fig. 5; Fig. 8 = Pl. 6, fig. 1; Fig. 9 = Pl. 6, fig. 2; Fig. 10 = Pl. 6, fig. 3; Fig. 11 = Pl. 6, fig. 4; Fig. 12 = Pl. 6, fig. 5. Figs. 13–15. *Baculites subanceps* Haughton. Fig. 13 = Pl. 5, fig. 3; Fig. 14 = Pl. 6, Fig. 6; Fig. 15 = Pl. 6, fig. 7.

All figures natural size.

The rounded shape of the venter in *B. subanceps* is sufficient to separate it specifically from *B. anceps*, for the keel or sharpened venter of the latter is the one constant character of an otherwise variable species. No intermediate examples occur in the type poluations of either species. The Angolan examples described belong to the subspecies *B. subanceps subanceps*. In the Pacific region a second subspecies occurs, *B. subanceps pacificus* Matsumoto & Obata, which was originally described as a subspecies of *B. anceps*. However it has the rounded venter of *B. subanceps* with no trace of sharpening as in *B. anceps*. The Pacific subspecies differs from the type subspecies in Angola in having many more closely spaced arcuate ribs on the side of the shell. Comparison of the holotype of *pacificus* (Matsumoto 1959*a*: pl. 34, fig. 3) with the lectotype of *subanceps* (Pl. 6, fig. 6) shows that *pacificus* has between two and three times as many arcuate ribs as *subanceps*. The density of the ribs on the venter is approximately the same in the two subspecies, as is also the whorl shape, the shape of the mouth border and the curve of the ribbing. There are no other differences between the two forms, which appear to be genuine contemporaneous subspecies that are geographically separate. *B. subanceps pacificus* can be dated as Upper Campanian in both Japan and California, while *B. subanceps subanceps* is definitely of Upper Campanian age in Angola, as deduced from the associated *Libycoceras* and the many heteromorph ammonites.

The only other *Baculites* known from Angola are the fragments with keeled or sharpened venters described by Haughton (1925: 279, pl. 14, fig. 9), and the apparently similar forms described by Haas (1943: 13–15, figs. 15–19) as *B. anceps*, all from localities near Capolo. They are poorly preserved and from the wide variety of forms of the venter, some distortion has probably occurred making specific determination doubtful. Two Middle or Upper Campanian specimens from Madagascar figured by Collignon (1938: 88, pl. 6, figs. 4, 5) are also poorly preserved and of doubtful affinities. The Pondoland and Zululand *Baculites* described by Woods (1908) and Spath (1921*a*) and further Madagascan species described by Collignon (1931) all appear to be of Santonian age, and the only other high Cretaceous specimen known from south of Sahara is the example from the Maastrichtian of Nigeria figured by Reyment (1955: 15, pl. 1, fig. 5) as *B.* cf. *asper* Morton.

The most closely related species to *B. subanceps* is the Polish Upper Campanian species *B. leopoliensis* Nowak (1908: 328, pl. 14, figs. 1–5, 10), which differs in that its arcuate ribs are retained to a large size (at least 40 mm. cross section height), its ribs do not form marked chevrons on the venter, and the thickest part of the arcuate ribs are approximately at the centre of the side, not dorsal as in *B. subanceps*. *B. palestinensis* Picard (1929: 438, pl. 10, figs. 1–7) is another closely related species from the Upper Campanian of Israel; its ribs are less strongly curved and less projected on both venter and dorsum than in *B. subanceps*, and the thickest part of the arcuate rib is in the middle of the side. The Alpine species *B. fuchsi* Redtenbacher (1873: 134, pl. 30, fig. 15) and the Californian species *B. fairbanksi* Anderson (1902: 92, pl. 7, figs. 152, 153; 1958: 190, pl. 49, fig. 4) are both based on holotypes that are too poorly preserved to be interpreted satisfactorily, as has been pointed out by Matsumoto (1959*a*: 134).

Family **NOSTOCERATIDAE** Hyatt 1894

The difficulties in arriving at a satisfactory generic classification of this family have been pointed out by Anderson (1958: 195) and Matsumoto (1959*a*: 157–158). The character usually considered to be of greatest generic significance is the mode of coiling of all the whorls, and especially of the adult body chamber; the presence or absence of tubercles, constrictions and flared ribs are characters used to a lesser extent. The classification arrived at by Wright (1957: *L* 222–224) is based mainly on mode of coiling and is a sound division of the family. Although few species of Nostoceratidae are known from large collections, in those where ten or more specimens are known from a single locality (including the Angolan collections of *Didymoceras subtuberculatum* sp. nov. and *Nostoceras hyatti* Stephenson described below), the mode of coiling shows little variation. At species level it is no more variable than any other ammonite character, and groups of species with similar coiling make satisfactory generic divisions. But considerable difficulties arise with the Campanian–Maastrichtian genera *Cirroceras* Conrad (1868), *Didymoceras* Hyatt (1894), *Nostoceras* Hyatt (1894) and *Bostrychoceras* Hyatt (1900), to which all the Angolan examples belong, and these will have to be discussed more fully here. Wiedmann's (1962) solution was to refer all these forms to the oldest of them, *Cirroceras* (*Jouaniceras* Basse 1939, was also included as a synonym), but it is open to the objections that *Cirroceras* is not generically identifiable, *Nostoceras* is a compact and useful group of species, and the type species of *Bostrychoceras*, *B. polyplocum* (Roemer), was somewhat mis-interpreted by Wiedmann.

Cirroceras Conrad (1868). Type species: *Ammonceratites conradi* Morton (1841). The holotype is from the Upper Campanian or Lower Maastrichtian of New Jersey, and is a fragment of less than one whorl from the middle growth stage of the ammonite. It is poorly preserved, crushed and seems to have been non-septate. It was refigured by Whitfield (1892: 269, pl. 45, figs. 9–11), and is now apparently lost, but figures of a plaster cast of it have recently been given by Reeside (1962: 120, pl. 70, figs. 1–3). Other specimens referred to Morton's species by Whitfield (1892: pl. 45, figs. 12, 13) and Weller (1907: 833, pl. 108, figs. 5–8) belong to the well-known species *Nostoceras hyatti* Stephenson. Identification of *Cirroceras* must rest on the holotype alone, but it is clearly too fragmentary to distinguish between *Didymoceras* and *Emperoceras*. It closely resembles one of the superb specimens of *Emperoceras simplicicostatum* figured by Whitfield (1902: 68, pl. 25, fig. 2), but it could equally well be one of several species of *Didymoceras* (e.g. *D.* (?) *newtoni* Whitfield 1880: 449, pl. 15, figs. 1–4, or *D. hornbyense* (Whiteaves), Usher 1952: 103, pl. 27, figs. 1, 2, pl. 28, fig. 2), or a *Nostoceras* such as *N. draconis* Stephenson (1941: 413, pl. 82, figs. 5–9). (*Emperoceras* is quite distinct from the other genera (*Didymoceras*, *Bostrychoceras* and *Nostoceras*) described here because of its two long parallel arms in early growth stages (Whitfield 1902)). Discovery of more complete specimens from the same horizon and locality would hardly settle its identity satisfactorily, because the doubt would always remain as to whether they really were the same as the holotype. The absence of early and of adult whorls precludes generic identification, and *Cirroceras* must therefore be considered a *nomen dubium*, an unusable generic name.

Apart from *Nostoceras* which forms a compact, closely defined group (discussed below), there remain a large number of species to which the names *Didymoceras* and *Bostrychoceras* have been applied with differing interpretations and limits. The question to be decided is whether species such as *B. elongatum* (Whiteaves) (Usher 1952: pl. 28, figs. 3, 4), usually considered typical of *Bostrychoceras*, are to be separated generically from those like *D. hornbyense* (Whiteaves) (Usher 1952: pl. 27; pl. 28, fig. 2), usually considered typical of *Didymoceras*. The complete range of variation is perhaps better illustrated by two specimens figured by Stephenson (1941: pl. 83, figs. 6, 7 and fig. 13) that are very different, and would be referred to different genera by most workers. There are many species representing different combinations of tight or loose coiling and presence or absence of tubercles or constrictions between these extremes, and when the type species of *Didymoceras* and *Bostrychoceras* are examined, both are found to be relatively close to the centre of the variation.

Didymoceras Hyatt, 1894. TYPE SPECIES: *Ancyloceras nebrascense* Meek & Hayden 1856. The holotype (Meek 1876: 480, pl. 22, fig. 1) is a half whorl fragment in which the whorls were probably in contact. A better specimen was figured by Whitfield (1880: 451, pl. 14, fig. 9, pl. 15, fig. 6) and consisted of two helically coiled whorls in contact. In the specimen figured by Hyatt (1894: 574, pl. 14, figs. 13, 14) only the last helical whorl before the body chamber is preserved; this is not in contact and is followed by a rounded body chamber loop. Regular bituberculation is present on the body chamber and the last one or two whorls of the spire. Another typical species is *D. hornbyense* (Whiteaves 1895) (Usher 1952: 103, pl. 27, pl. 28, fig. 2), in which only the last whorls of the spire are loosely coiled.

Bostrychoceras Hyatt, 1900. TYPE SPECIES: *Turrilites polyplocus* Roemer 1841. Wiedmann's (1962: 198–200) interpretation of this species is open to criticism. Roemer (1841: 92, pl. 14, figs. 1, 2) figured two syntypes of his species, and Schlüter (1872: 112) specifically excluded Roemer's fig. 2 from his synonymy of this species. But this can hardly be considered as a selection of Roemer 1841, pl. 14, fig. 1 as lectotype of the species, because in the next part of his work Schlüter (1876: 135) included the same fig. 1 of Roemer (and again specifically excluded fig. 2) in a new species *T. saxonicus*. This is not corrected in the corrigenda to Schlüter's work, and from his wide interpretation of *T. polyplocus* it is not clear which of Roemer's two figures he wished to include in the species. Wiedmann (1962: 198) must be credited with having selected Roemer's fig. 1 as lectotype. This lectotype has very irregular tubercles only on its last whorl just before it becomes uncoiled, and from the way they are drawn it could even be doubted whether they are tubercles at all. At least the whole of the closely coiled spire is non-tuberculate in a typical *B. polyplocum*. Of the specimens figured by Schlüter (1872) the two non-tuberculate specimens of pl. 33, figs. 3 and 4 are the most typical of *B. polyplocum*, while pl. 33, fig. 5 has the last three whorls loosely coiled and tubercles on the body chamber. The remainder might all be different species—pl. 33, fig. 6 and pl. 35, fig. 8 are bituberculate and loosely coiled, pl. 34, fig. 1 is similar but tightly coiled at large sizes, pl. 33, fig. 8 is constricted and probably tightly coiled, pl. 34, figs. 2–5 has depressed whorls and has been re-named *Cirroceras depressum* Wiedmann (1962: 199), and pl. 35, figs. 1–7 have been referred by Wiedmann (1962: 204) to *Didymoceras schloenbachi* (Favre). The species *B. secoense* Young (1963) from Texas differs from *B. polyplocum* only in being consistently bituberculate on all whorls. Further work on much larger collections from Germany is necessary to determine the limits of variation in *B. polyplocum*, but it seems most likely that the tightly coiled, non-tuberculate forms and those with the last one or two whorls loose and tubercles on the body chamber, are conspecific. A fine specimen of the former type from Madagascar was figured by Boule, Lemoine & Thevenin (1907: 61, pl. 14, fig. 1). *B. indicum* (Stoliczka) (Kossmat 1895: 143), to which Wiedmann (1962: 200) referred these tightly coiled, non-tuberculate forms, differs in having constrictions on all whorls and is of Coniacian to Santonian age. Matsumoto's (1959*a*: 159) suggestion that the constricted group being Santonian and older might be separated subgenerically from the non-constricted group which are Campanian and Maastrichtian, seems to be defeated by the presence in the Maastrichtian of such strongly constricted forms as *B. saundersorum* (Stephenson 1941: 416, pl. 83, figs. 6–8). Another typical species of *Bostrychoceras* is *B. elongatum* (Whiteaves) (Usher 1952: 105, pl. 28, figs. 3, 4).

Thus the type species of *Didymoceras* and *Bostrychoceras* are very similar, differing only in the slightly looser coils and more persistent tubercles of the former. The difference does not warrant generic separation. A form which is perhaps midway in morphology between the two type species is *D. californicum* Anderson (1958: 197, pl. 72, fig. 6). A large number of other forms carry the range of variation far beyond the characters of the two type species. *B. condamyi* (Collignon 1932: 39, pl. 9, figs. 1, 2) and *B. otsukai* (Yabe 1904: 14, pl. 3, fig. 9, pl. 4, figs. 1–3) have ribbing like a typical *Bostrychoceras* but loosely coiled whorls. A specimen of the latter species figured by Matsumoto (1959*a*: 160, pl. 40, fig. 2) differs from a typical *Didymoceras* (e.g. Usher 1952: pl. 27) only by its finer ribs and lack of tubercles. *B. boulei* (Collignon, 1932: 40, pl. 9, fig. 4) has fine ribs and no tubercles, but very loosely coiled whorls. *D. navarroense* (Shumard) (Stevenson 1941: 417, pl. 83, figs. 9–13) is equally loosely coiled but has heavy bituberculation; while *D. subtuberculatum* sp. nov. described below has smaller tubercles and periodic flared ribs. Amongst the closely coiled species, *D. stevensoni* (Whitfield 1880) is typical of *Didymoceras* except that some examples (Whitfield 1901: 219, pls. 29, 30) are closely coiled up to the end of the final whorl, *B. colubriformis* (Stevenson 1941: 412, pl. 81, figs. 1–3) is dwarf and has constrictions and fine bituberculate ribs, and *B. saundersorum* (Stevenson 1941: 416, pl. 83, figs. 6–8) is particularly tightly coiled, non-tuberculate and has marked constrictions. *D. schloenbachi* (Favre 1869; see Basse 1931: 19, pl. 2, figs. 11–15; Wiedmann 1962: 204) is equally tightly coiled, but is bituberculate and constricted and as its body chamber is not known it might be a *Nostoceras*. In addition there are many fragmentary specimens described under different specific names by Gabb (1864), Meek (1876) and Anderson (1958) that are not even generically identifiable.

The three main variables—coiling (loose or tight), tubercles and constrictions (present or absent in each case)—give eight different combinations, to each of which one or more species could be referred. To use coiling alone as the basis for generic division would leave a large number of intermediate species that have partly loose whorls. As the choice is between one genus or about eight genera, all these forms are best referred to *Didymoceras* Hyatt, of which *Bostrychoceras* Hyatt is considered a subjective synonym.

Nostoceras Hyatt 1894. Type species: *N. stantoni* Hyatt. The two syntypes were figured by Stephenson (1941: 407, pl. 80, figs. 2–5) together with several other species of the genus. This is a relatively closely defined genus, characterized by a closely coiled spire followed by a U-shaped retroversal body chamber that breaks away suddenly from the spire. In *Nostoceras* s.s. the body chamber hangs vertically below the spire, in the subgenus *Anaklinoceras* Stephenson (1941: 414) it turns upwards and surrounds the spire. All have well developed bituberculate ribbing on all whorls. Most of the known species are the North American forms described by Anderson & Hanna (1935: 22), Stephenson (1941) and Anderson (1958). In addition there are the Angolan forms described below, some undescribed badly crushed examples from Syria and Iraq, and possibly *N. schloenbachi* (Favre 1869—see above), *N. pauper* (Whitfield) (Reeside 1962: 118, pl. 68, figs. 10–13), *N. natalense* (Spath 1921*a*: 248, pl. 22, fig. 2) and *N. subangulatum* (Spath 1921*a*: 250, pl. 22, fig. 3) of which the body chambers are not known.

In the descriptions of the Angolan fauna the following terms are used for the helically coiled forms. With the spire in an upright position and the apex pointing upwards, the *upper* part of the whorl is the upper surface between the venter (the siphuncle is usually just above the outermost point of the whorl) and the dorsum, the *lower* part of the whorl is the lower surface between venter and dorsum. When the whorls become detached and form a U-shaped loop as in *Nostoceras*, the ornament of the spire becomes twisted so that what was the upper part of the whorl forms the *back* of the loop, while what was the lower part of the whorl forms the *front* of the loop. The venter runs around the periphery of the loop (or occasionally just to the back of the periphery).

Genus ***DIDYMOCERAS*** Hyatt 1894

Didymoceras subtuberculatum sp. nov.

Plate 7, figs. 2–6, Pl. 11, fig. 4

Holotype. C. 52701 (Pl. 7, fig. 2) from 1 km. north of Egito, Angola.

Material. In addition to the holotype, 16 specimens, including 15 paratypes (C. 52693, C. 52695–709) and C. 52694 which shows some variation. Same locality.

Diagnosis. The spire consists of a loose helicoid spiral, dextrally or sinistrally coiled, distance between adjacent whorls in uncrushed material roughly equal to cross section diameter of shell at that point. Earliest whorls and shape of adult body chamber not seen in material preserved. Whorl section approximately circular at all growth stages seen. Ornament consists of ribs, tubercles, constrictions and flared ribs, all developed at all growth stages. Ribs fine and dense and not interrupted on either venter or dorsum; they cross the dorsum radially, are inclined backwards on both upper and lower sides in crossing from dorsum to venter, but the inclination is considerably more on the upper side, so that they are inclined forwards in crossing the venter from upper to the lower side. Occasional ribs bifurcate on upper and lower sides and a few intercalated ribs cross the venter. Three or four flared ribs per whorl, present on all the whorls preserved, flares often immediately preceded by a slight constriction. Two rows of tubercles occur on all whorls; upper row just below mid-ventral line (i.e. line of siphuncle) and lower row just ventral of middle of lower surface. These paired tubercles joined by two ribs with 2 to 6 non-tuberculate ribs between each pair; much more widely spaced flared ribs usually coincide with tubercle spacing and are therefore tuberculate.

Remarks. Of the 17 fragmentary specimens of this species, 10 are dextrally coiled and 7 sinistrally coiled. Only a few are not distorted or crushed. Four of the smallest specimens that are relatively uncrushed (Pl. 7, figs. 4, 5) show a loose helical spiral that must be close to the original shape of the conch. Two of the medium-sized specimens are crushed by pressure along the axis of the spire so that the whorls are nearly in contact, but one of these is selected as holotype for its has 1½ complete whorls and shows the characters of the species better than any other specimen (Pl. 7, fig. 2). Two other specimens are crushed by pressure at right angles to the spire axis and are less well preserved (Pl. 7, fig. 3). The largest specimens are only short fragments but are not badly crushed and show the whorl shape and ornament well (Pl. 7, fig. 6). The largest and smallest whorls preserved have cross section diameters of 43 mm. and 7 mm. respectively. Suture-lines are poorly preserved and difficult to follow in all specimens, but septal surfaces up to 40 mm. diameter occur in several of the large specimens, indicating that adults reached sizes at least a half to one whorl larger than the largest fragment preserved. None of them shows evidence of modified adult body chamber coiling. Significant variation from the remainder of the collection can only be seen in one specimen: C. 52694 is a short septate fragment with a whorl section diameter of 34 mm., and has particularly strongly curved and oblique ribs which do not appear to have any tubercles.

Spath (1951: 8; 1953: 49) made two specific determinations for these specimens: "*Bostrychoceras polyplocum* (Römer) Schlüter, pars" and "*Bostrychoceras* sp. nov. (cf. *punicum?*, Pervinquière)". The second determination can be discarded for it was presumably given to some of the smaller specimens, which after extraction from the matrix have proved to be the same as the remainder of the collection. The reference to part of Schlüter's interpretation of *Didymoceras polyplocum* is presumably to the bituberculate and loosely coiled specimens (Schlüter 1872: pl. 33, fig. 6, ? pl. 34, fig. 1, pl. 35, fig. 8) that have been shown above (p. 372) to be different from the restricted *D. polyplocum*. There are no flared ribs on these specimens and only one of them (pl. 35, fig. 8) has a constriction on what appears to be the body chamber, so they are probably specifically distinct from the flared and constricted Angolan forms. In fact the 17 specimens of *D. subtuberculatum* show little variation, and the specific diagnosis drawn from them is certainly not wide enough to include the German forms.

There are few other Campanian or Maastrichtian forms that are closely comparable with *D. subtuberculatum*. The Pondoland and Zululand specimens figured by Woods (1906: 339, pl. 42, figs. 4, 5) and Spath (1921*a*: 252, pl. 24, fig. 2) appear to be loosely coiled and two of them have flared ribs, but none has any tubercles and they are only small fragments. Several loosely coiled examples from Madagascar figured by Collignon (1932: 40, pl. 9, fig. 4; 1938: 87–88, pl. 5, fig. 4, pl. 6, fig. 2) are also without tubercles or flares.

At first sight *D. subtuberculatum* seems to resemble several Turonian to Santonian species of *Hyphantoceras*, such as the Japanese species *H. venustum* (Yabe 1904: 11, pl. 5, figs. 1, 2 (holotype), pl. 3, fig. 4—*Euhyphantoceras maestrichtiense* Shimizu 1935, is an objective synonym and is Santonian, not Maastrichtian) and the north American species *H. buttense*, *H. ceratopse* and *H. laqueum* described and figured by Anderson (1958: 207–210), all of which might be synonyms of *H. venustum* (see Matsumoto 1959*a*: 158). There is even some resemblance to Schlüter's figures (1872, pl. 32, figs. 13–20) of the type species *Hyphantoceras reussianum* (d'Orbigny). In *Hyphantoceras*, however, the arrangement of the ornament is different; the flared ribs are more frequent and each bears 2 to 4 tubercles, while all the ribs between the flares are non-tuberculate; in *D. subtuberculatum* the flares are fewer and more widely spaced, and tubercles occur at smaller intervals on non-flared as well as flared ribs.

***Didymoceras* cf. *californicum* Anderson**

Plate 8, fig. 1

1958 *Didymoceras californicum* Anderson: 197, pl. 72, fig. 6.

MATERIAL. One specimen, C. 52727, from Carimba, Angola.

DESCRIPTION. The specimen consists of one and a quarter coiled whorls and part of another smaller whorl. The whorls are in contact, and siphuncle and septa occur up to the largest stage preserved. The whorl section is approximately circular and the diameter of the largest whorl is 23 mm. The ornament consists of simple ribs, approximately 42 per whorl, which cross the venter inclined at an angle to the whorl but roughly parallel to the axis of the spire. The ribs bear two rows of small insignificant tubercles; the upper row is exactly along the line of the siphuncle, while the lower row is some distance below this. Only one rib bifurcates at a tubercle in this specimen, all the remaining ribs being single.

REMARKS. This specimen and Anderson's species are readily compared with *Didymoceras polyplocum* (Römer) and *D. elongatum* (Whiteaves). The differences between the three species are mainly the density of the ribs, and the occurrence of small tubercles on the septate whorls of *D. californicum*. At approximately the size of the specimen described here, the rib density is 25 per whorl in the lectotype of *D. elongatum* (Usher 1952: 105, pl. 28, fig. 3), about 42 per whorl in the present specimen, and 55–60 per whorl in *D. polyplocum* (Römer 1841: pl. 14, fig. 1; Schlüter

1872: pl. 33, figs. 3–5). The Angolan specimen differs from the other two species by its regular small tubercles (in *D. polyplocum* tubercles are irregular and rare on all whorls before the body chamber). Anderson's holotype (the only specimen) came from the Upper Campanian or Lower Maastrichtian of California, and shows the uncoiled body chamber commencing at about the maximum size attained by the Angolan specimen. Agreement in whorl section, coiling and ornament is close, except that rib bifurcation at tubercles is probably more common in the Californian specimen.

The only comparable African specimens are those figured by Basse (1931: 18, pl. 1, figs. 16, 17) from Madagascar and by Reyment (1955: 15, pl. 1, fig. 4) from Nigeria; both are Maastrichtian, but are fine-ribbed and closer to *D. polyplocum* than to the Angolan specimen.

The Texan species *D. secoense* (Young 1963: 42, pl. 3, figs. 1–5, pl. 4, figs. 4, 8; Adkins 1928: pl. 37, figs. 1, 3) differs from *D. polyplocum* only in its possession of regular bituberculation on every second or third rib. It resembles *D. californicum* but its rib density is greater.

It seems unlikely that *D. californicum* is a synonym of *D. hornbyense* (Whiteaves) as claimed by Matsumoto (1960: 54), for it has a considerably smaller apical angle, its tubercles are much smaller, and it shows no evidence of slow loosening of the last one or two septate whorls before the body chamber as in *D. hornbyense*.

***Didymoceras* cf. *hornbyense* (Whiteaves)**
Plate 8, fig. 4

1895 *Heteroceras hornbyense* Whiteaves: 316.
1903 *Heteroceras hornbyense* Whiteaves: 332, pl. 42, figs. 1–4.
1921*a* *Didymoceras hornbyense* (Whiteaves) Spath: 251.
1925 *Didymoceras hornbyense* (Whiteaves); Haughton: 276, pl. 15, fig. 2.
1952 *Nostoceras hornbyense* (Whiteaves); Usher: 103, pl. 27, figs. 1, 2, pl. 28, fig. 2, pl. 31, fig. 23.

MATERIAL. One body chamber fragment, C. 52737, from Barra do Dande, Angola.

REMARKS. The single specimen is well preserved with neither distortion nor crushing, and consists of a quarter of a whorl of body chamber 95 mm. long with the last septum preserved. The whorl section is circular, 27 mm. diameter at the smaller end, 33 mm. at the larger end. The coiling is dextral. Towards the smaller end the venter is considerably eroded and the ribs and tubercles almost removed. On the dorsum the ribs are reduced to small striae. Pairs of large tubercles occur irregularly on every third or fourth rib, and there are some looped ribs between the tubercles.

Another fragmentary example from Angola, figured by Haughton, is smaller than the present specimen, but has closely similar ornament. Both specimens show the typical characters of *D. hornbyense* as seen in Whiteaves' original specimens and Usher's (1952: 103) revision. The example figured here compares well with the largest figured by Usher (1952: pl. 27). Reference to *Didymoceras* rather than to *Nostoceras* is favoured on account of the large size of the body chamber, which does not form the hanging U-shaped body chamber characteristic of *Nostoceras*. Its possible relationship with *N. helicinum* is discussed below.

Didymoceras cf. ***angolaense*** (Haughton)
Plate 8, fig. 2

1925 *Nostoceras angolaense* Haughton: 275, pl. 15, fig. 1.
?1943 *Nostoceras* cf. *angolaense* Haughton; Haas: 5–6, figs. 2, 8.

MATERIAL. One specimen, C. 52739, from Barra do Dande, Angola.

REMARKS. The specimen consists of four whorls closely coiled into a dextral helical spire of small apical angle. The whorl section is rounded between the ribs, but is angular over the tubercles as described by Haas (1943: 5, fig. 2). The ribs, tubercles and constrictions are similar to those in the type specimen described by Haughton, although the 20–22 tubercles in each row of the present specimen appear to be slightly more than in the holotype. There are 33 ribs on the last whorl, but no suture-lines can be seen in this specimen, which is preserved as a limonite-stained shell filled with crystalline calcite. The specimens described by Haas are fragmentary and have no distinct ribs, and cannot be referred with certainty to this species.

The species is referred to *Didymoceras* rather than to *Nostoceras* because the last whorl of the holotype is loose, and does not change suddenly to the downwards curving body chamber typical of *Nostoceras*. The most closely related species are *D. splendidum* (Shumard) (Stephenson 1941: 415, pl. 82, figs. 1–4) from the Lower Maastrichtian of Texas and *D. excelsus* (Anderson 1958: 194, pl. 72, fig. 4) from the top of the Campanian or the Lower Maastrichtian of California. Both these species differ in having even more acutely angled spires, a pair of tubercles on each rib and no non-tuberculate ribs as in *D. angolaense*.

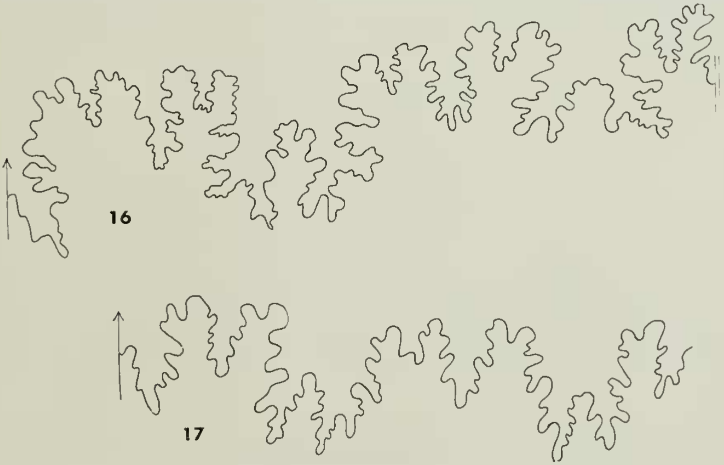
Genus ***NOSTOCERAS*** Hyatt 1894

Nostoceras hyatti Stephenson
Plate 9, Pl. 10, fig. 1; Text-fig. 16

1892 *Heteroceras conradi* (Morton); Whitfield: 269–271, pl. 45, figs. 12, 13, *non* figs. 9–11, 14.
1907 *Heteroceras conradi* (Morton); Weller: 833, pl. 108, figs. 5–8.
?1935 *"Hamites" vancouverensis* Gabb; Anderson & Hanha: 23, pl. 7, figs. 2–4, pl. 8, fig. 5.
1941 *Nostoceras hyatti* Stephenson: 410, pl. 81, figs. 9–12.
1951 *Didymoceras* sp. nov. ind., Sornay: 274, pl. 4, fig. 4.
1962 *Nostoceras* sp., Reeside: 119, pl. 69, figs. 7–12.

MATERIAL. 10 specimens, C. 52740–43, C. 52747–52, from Barra do Dande, Angola.

DESCRIPTION. The collection consists of seven looped body chambers, one having the last spiral whorl preserved, the other six having a short septate portion or the last septum preserved and the entire spire missing, and three fragments of body chambers. The spire is coiled dextrally in four specimens and sinistrally in three (the coiling is not determinable in the three fragments). The last whorls of the spire are in contact right up to the point at which the rapid change to the U-shaped body chamber occurs. The two limbs of the body chamber are nearly straight and close together, leaving only a narrow gap between them which diminishes in width at the level of the mouth border. The length of the body chamber varies slightly, for in some the last septum is at the beginning of the first straight arm opposite the mouth border, while in others it occurs earlier at about the position at which the whorl breaks away from the closely coiled spire. The axis of the spire is inclined at a small angle (*c.* 20°) to the plane of the body chamber. The whorl section is approximately circular throughout although the diameter at right angles to the plane of the body chamber increases on the middle part of the body chamber in most examples. The ribs are sharp and mainly single throughout but occasional irregular bifurcation occurs at the tubercles or at the edge of the dorsum, and irregular looping or zigzagging occurs between some of the tubercles. The strength of the ribbing is considerably reduced on the dorsum of all whorls. On the body chamber the ribs are markedly stronger and more widely spaced than on the spiral whorls but they tend to increase in density again on approaching the mouth border. On the spiral whorls the ribs are inclined at a small angle to a whorl section plane; on the body chamber ribs are generally more radial (i.e. annular) but they are somewhat irregular and on the back part (see descriptive terms for helically coiled ammonites p. 374 above) of the first straight limb the ribs are arched upwards and particularly strong. Narrow constrictions occur at wide intervals on the spiral whorls, but not on the main part of the body chamber. The mouth border is immediately preceded by a constriction, then a collar-like rib, followed by a narrow flat portion up to the slightly sinuous mouth border. Two rows of medium sized tubercles occur fairly constantly on alternate ribs on the spiral whorls; the upper row overlies the siphuncle, the lower row occurs just below the line of contact between adjacent whorls. On well preserved parts complete with the shell the tubercles are elongated into short pointed spines. On the body chamber the tubercles occur on every rib, gradually



Figs. 16, 17. Suture-lines of *Nostoceras*. Fig. 16. *Nostoceras hyatti* Stephenson. Last suture-line of an adult at 21 mm. ventro-dorsal diameter. C. 52743, from Upper Campanian, Barra do Dande, Angola. ×3. Fig. 17. *N. obtusum* sp. nov. Suture-line at 10 mm. ventro-dorsal diameter. Holotype, C. 52744, from Upper Campanian, Barra do Dande, Angola. ×5.

increasing in size to become large round the U-shaped bend, then rapidly diminishing towards the mouth border. The line of the two rows moves outwards on the first part of the body chamber until they are situated on the periphery of the main bend and the final limb of the body chamber. One dextrally coiled specimen shows half a complete suture-line lying to the right of the siphuncle and the left of the dorsum (i.e. on the "top" of the whorl) (Text-fig. 16). The first and second lateral saddles are similar in shape and size, both being divided into two by a minor lobe of moderate depth then each half divided into two again. The dorso-lateral saddle is smaller, but is also bifid and is bounded by the short narrow dorsal lobe in the middle of the dorsum. The first and second lateral lobes are large and deep and each is divided by a large minor saddle.

The largest and smallest specimens have mouth border diameters of 27 mm. and 22 mm., while the transverse and ventro-dorsal diameters in the middle of the loop of the largest specimen are 29 mm. and 23 mm. respectively. The distance between the mouth border and the lowest point of the periphery of the loop varies between 45 and 65 mm. The largest diameter of the single helically coiled whorl preserved is 37 mm. at the point of break away of the body chamber, and at this point the cross section diameter is 17 mm.

REMARKS. None of the determinations given by Spath (1951: 10; 1953: 50) appears to fit these specimens. Stephenson's originals consist of both spire and body chamber from the top Campanian or Lower Maastrichtian of Texas, and the Angolan examples agree with them in all respects. The other specimens listed in the synonymy are all body chambers only. Whitfield, Weller and Reeside figured five fine body chambers from New Jersey that show the normal characters of *N. hyatti*; the interpretation of *Heteroceras conradi* (Morton) has been discussed above (p. 371)—it cannot be shown to be a *Nostoceras* and it is certainly not conspecific with *N. hyatti*. The two body chamber fragments from California figured by Anderson & Hanha also agree closely with *N. hyatti*; the interpretation of *Hamites vancouverensis* Gabb (1864: 70, pl. 13, fig. 18) is difficult because the holotype is a small fragment, and again it is most unlikely to be the same as *N. hyatti* because of its larger size and different tuberculation. Matsumoto (1960: 54) was probably correct in uniting *H. vancouverense*, *Didymoceras fresnoense* and *Exiteloceras bennisoni* of Anderson (1958: 197, pl. 68, fig. 2; 201, pl. 72, fig. 7); all differ from *Nostoceras* in their open or rounded-U-shaped body chambers, and belong to either *Didymoceras* or *Emperoceras*. Another North American top Campanian or Lower Maastrichtian species, *Ammonites cooperi* Gabb (1864: 69, pl. 14, fig. 23), included in *H. vancouverensis* by some authors, is also difficult to interpret because of a fragmentary holotype. The interpretations of Whiteaves (1903: 336, pl. 43, fig. 1) and Usher (1952: 107, pl. 29, fig. 1) are probably correct and put *A. cooperi* into the genus *Emperoceras*. Finally the single body chamber figured by Sornay (1951: 274, pl. 4, fig. 4) is from Barra do Dande, Angola, and is a good example of *N. hyatti*. It closely resembles one of the examples figured here (Pl. 10, fig. 1).

Nostoceras hyatti is characterized by its large size and bold ribs and tubercles. *N. sternbergi* Anderson & Hanha (1935: 22, pl. 7, fig. 1) differs in having finer ribs and smaller tubercles, *N. draconis* (Stephenson 1941: 413, pl. 82, figs. 5–9) has finer ribs and a depressed spire of high apical angle, *N. kernense* (Anderson 1958: 196, pl. 65, fig. 1) has regular plicate ribbing, and *N. mexicanum* (Anderson 1958: 196, pl. 58, fig. 3) has finer ribs and small irregular tubercles. The species is known only from Texas, New Jersey, California and Angola.

***Nostoceras* cf. *kernense* (Anderson)**

Plate 8, fig. 6

1958 *Didymoceras kernense* Anderson: 196, pl. 65, figs. 1, 2.

MATERIAL. One specimen, C. 52746, from Barra do Dande, Angola.

REMARKS. This fragment of a U-shaped body chamber is compared with Anderson's species because of its markedly branching ribs. It can be seen from the figure that the position of branching, density and angle of the ribs show a close resemblance to Anderson's holotype. In some places the branching is virgatotome with up to three secondary ribs leaving the primary rib in succession. The Angolan specimen differs in being considerably smaller and by having shorter straight arms on the body chamber (judging from the rapid narrowing of the gap between them). In a few places where the shell is preserved the ribs can be seen to cross the venter as in Anderson's holotype, but most of the specimen is an internal mould on which the band between the rows of tubercles is nearly smooth.

The only comparable species is *N. sternbergi* Anderson & Hanha (1935: 22, pl. 7, fig. 1) from California. This shows similar multiple rib branching, but it has constrictions and differs in details of ribbing, including a sudden change to bold ribs on the final straight limb.

***Nostoceras rotundum* sp. nov.**

Plate 10, fig. 3

1951 *Didymoceras angolaense* Sornay: 274, pl. 4, figs. 1–3.

HOLOTYPE. C. 52745, the only specimen, from Barra do Dande, Angola.

DIAGNOSIS. Medium sized species of *Nostoceras*, with close-coiled helical whorls, followed by a hanging body chamber consisting of a semicircular loop. Ornament on helical coils consists of 14 to 15 tubercles per whorl and weak ribs; tubercles and moderately strong ribs on body chamber.

DESCRIPTION. The single specimen in the present collection consists of three whorls closely coiled into a dextral spire, followed by a body chamber loop which breaks suddenly away from the spire and is angled obliquely downwards forming a nearly perfect semicircular loop; the mouth border faces obliquely upwards towards the last whorl of the spire. Suture-lines are too poorly preserved to reveal details, but the last suture-line is clearly seen to occur on the penultimate whorl directly above the point at which the loop leaves the spire, so that the body chamber consists of the whole of the last whorl of the spire plus the loop. The angle between the plane of the loop and the axis of the spire is 45°. Whorl sections in the spire are roughly circular with a small flat portion at the position of contact between whorls, and in the loop the transverse diameter is slightly greater than the ventro-dorsal diameter. Ornament consists of obliquely aligned pairs of tubercles forming two rows. On the spire the upper row forms the outermost point of the whorl and contains 14 tubercles per whorl, while the lower row occurs above the position of contact between whorls and contains 15 tubercles per whorl. The tubercles increase slightly in strength on the loop and the rows twist so that the lower row occurs around the outermost periphery of the loop, while the upper row goes onto the back of the loop. Ribs are poorly developed on all whorls. Between the rows of tubercles on the spire and the loop only vague undulations occur, but above and below the rows of tubercles weak ribs occur on the spire, and these strengthen on the loop to form simple curved ribs above the upper row and both simple and plicate ribs below the lower row. The dorsum of the loop is smooth. The siphuncle occurs just above the upper row of tubercles. No constrictions occur on any part, but just before the end of the body chamber the whorl contracts laterally, then flares out and ends in a gently sinuous mouth border of exactly circular section. Diameter of the mouth border 23 mm.; diameter of the semicircle of the loop 52·5 mm.; total height of specimen as preserved 88 mm.; total height extrapolated to apex 110–115 mm.; diameter of the final spiral whorl 40 mm.

REMARKS. From the description and figures of Sornay's single specimen from Barra do Dande it is difficult to identify his specimen with the one figured here. However Sornay's original was kindly made available on loan by Dr. L. Cahen, Director of the Musée royal de l'Afrique centrale, Tervuren, and the great similarities between the two were then revealed. Sornay's specimen consists of three-quarters of a whorl coiled into a sinistral helical spire, followed by a downwards twisting portion, then two-thirds of a semicircular loop. On the spiral whorl there is a marked depression where the whorls were in contact right up to the point where the body chamber breaks away suddenly from the spire. The final suture-line is at the beginning of the spiral whorl, so that the body chamber occupied three-quarters of the last whorl of the spire plus the loop. From a comparison with the holotype it is probable that the mouth border is only just missing; the pair of tubercles before the broken aperture are probably the last ones. The tubercles and ribs agree exactly with those of the holotype. The diameter of the final spiral whorl is 54 mm., and the cross section diameter close to the mouth border is 29 mm.

The two specimens described above agree in having a semicircular loop with no straight arms, a body chamber that occupies the last whorl of the spire as well as the loop, bold ribs on the last part of the loop, and large tubercles throughout. These characters serve to distinguish the species from *N. hyatti* which has distinct straight arms in the loop, a body chamber occupying only the loop, and ribs dominant over tubercles on all but the bend of the loop. Reference of *N. rotundum* to *Nostoceras* or *Didymoceras* is arbitrary, and it is included here in *Nostoceras* because of its tightly coiled spire and large tubercles. The new specific name, *N. rotundum*, is necessary because *N. angolaense* (Sornay 1951) is pre-occupied by *N. angolaense* Haughton, 1925. Specimen C. 52745 is chosen as holotype rather than Sornay's larger specimen because it is more complete and free from matrix.

N. mariateresianum Haas (1943: 6, 7, figs. 1*b*, 9), a closely related species from Angola, is known only from a single fragment that has similar ornament with dominant tuberculation, but has 22 to 24 tubercles per whorl in each row and 2 to 3 constrictions per whorl. Another Angolan species *Didymoceras angolaense* (Haughton), has a smaller apical angle, sharp ribs and small tubercles and a loose *Didymoceras* body chamber. The Zululand species *Nostoceras* (?)*subangulatum* (Spath 1921*a*: 250, pl. 22, fig. 3) has stronger ribs on the spiral whorls than in *N. rotundum*, and it is close to *Didymoceras* (or ?*Nostoceras*) *stevensoni* (Whitfield 1880: 447, pl. 14, figs. 5–8; 1901: 219, pls. 29, 30). Whitfield's (1901) figured specimen, though much larger, shows a similar loop to that of *N. rotundum.*

Nostoceras helicinum (Shumard)
Plate 8, figs. 3, 5

1861 *Turrilites helicinus* Shumard: 191.
1894 *Nostoceras helicinum* (Shumard) Hyatt, 573.
1941 *Nostoceras helicinum* (Shumard); Stephenson: 410, pl. 80, figs. 11, 12.
1943 *Nostoceras helicinum* (Shumard); Haas: 2–5, figs. 1*a*, 6, 7.

MATERIAL. Two specimens, C. 52738 and C. 52753, from Barra do Dande, Angola.

REMARKS. Both specimens are sinistrally coiled with the whorls in contact, the larger specimen, C. 52738, consisting of one whorl with a maximum diameter of 30 mm., the smaller specimen, C. 52753, consisting of nearly two whorls, the maximum diameter of the larger being 24 mm. Although suture-lines are not well preserved the larger specimen appears to have three-quarters of a whorl of presumably immature body chamber, while the smaller specimen is septate up to shortly before its aperture. Deep narrow constrictions occur at roughly 180° intervals on both specimens, and pairs of small tubercles are present on all whorls.

Two Angolan specimens were described and figured by Haas (1943: 2–5), and the two further specimens now figured agree with these in all respects. Haas's description was much more detailed and complete than that of Stephenson (1941: 410, pl. 80, figs. 11, 12) who designated the neotype of the species. The four Angolan specimens belong to the normal variety of *N. helicinum*, which has fine ribs and a spire angle of 80–90°. Two varieties that have been separated are *N. helicinum* var. *humile* Stephenson (1941: 412, pl. 81, figs. 4–6) which has a more depressed spire (larger spire angle) and rather coarser ribs and tubercles, and var. *crassum* (Stephenson 1941: 412, pl. 81, figs. 7, 8) which has much coarser ribs and tubercles. *N. stantoni* and its varieties (Stephenson 1941: 407–410, pl. 80, figs. 1–10) have a smaller spire angle and few tubercles, *N. hyatti* has a smaller spire angle and coarser ribs and tubercles, and the somewhat similar species *Didymoceras hornbyense* (Whiteaves) (Usher 1952: 103, pl. 27, pl. 28, fig. 2) attains much larger sizes and has larger ribs and tubercles.

Nostoceras (?) ***obtusum*** sp. nov.

Plate 10, fig. 2; Text-fig. 17

Holotype. C. 52744, the only specimen, from Barra do Dande, Angola.

Diagnosis. Coiled whorls consisting of depressed, obtuse-angled closely coiled spire; adult body chamber unknown. Two rows of tubercles are the dominant ornament, with small ribs crossing the whorl above and below them and low ribs connecting tubercles between rows.

Description. The single specimen consists of two whorls closely coiled into a sinistral helical spire that has a large apical angle of 125–130°. The first one and a quarter whorls are septate and the final three-quarters of a whorl is body chamber, probably that of an immature specimen, for the final septa are not approximated and there are no signs of adult body chamber modification of the mode of coiling. The whorl section has angles at the position of the tubercles, a flat or slightly impressed portion at the position of contact with earlier whorls just above the dorsum, and rounded upper and lower sides. Tubercles are the dominant feature of the ornament; the upper row occurs just below the mid-ventral line and forms the outermost point of the whorl, while the lower row occurs near the middle of the lower side and is the lowest point of the whorl. On the upper side of the whorl small straight radial ribs are connected to the tubercles in pairs, and on the dorsal side of the lower row of tubercles similar small ribs are connected singly or in pairs to the tubercles. These ribs are greatly reduced in crossing the dorsum. Between the two rows of tubercles low undulations join or occasionally zigzag between opposite tubercles; by comparison with the ribbed part of the whorl this band is nearly smooth. There are no constrictions. Maximum diameter of the final whorl 47 mm.; width of "umbilicus" on underside 20 mm.; whorl height (dorsum to top of outer tubercle) 15 mm.; the outer whorl has about 55 ribs on the upper side of the whorl, about 31 tubercles in the upper row, 25 tubercles in the lower row and 41 ribs on the lower side of the whorl. As much of the suture-line as is visible is shown in Text-fig. 17.

Remarks. The combination of a large apical angle, giving a very depressed spire, slender whorls, angled whorl section, and large tubercles with the lower row in the middle of the lower surface, serves to distinguish this species from any other *Nostoceras*. Other flat whorled species and varieties, such as *N. helicinum* var. *humile* Stephenson (1941: 412, pl. 81, figs. 4–6) and *N. draconis* (Stephenson 1941: 413, pl. 82, figs. 5–7, 8, 9), have much smaller tubercles and round whorl sections. The Zululand species *N.* (?) *natalense* Spath (1921*a*: 248, pl. 22, fig. 2) has much larger and more massive whorls, with large tubercles, bold ribs and a small "umbilicus" on the underside of the spire. *N. obtusum* is referred to *Nostoceras* rather than to *Didymoceras* because of the tight coiling and the ornament, which compare with other more completely known species of *Nostoceras*.

Family **DIPLOMOCERATIDAE** Spath 1926

Genus ***POLYPTYCHOCERAS*** Yabe 1902

Polyptychoceras pseudogaultianum (Yokoyama)

Plate 11, fig. 2

1890 *Ptychoceras pseudogaultianum* Yokoyama: 181, pl. 20, figs. 1, 2, ? 3.

MATERIAL. 10 specimens, C. 52718–26 from 1 km. north of Egito, and C. 52754 from Barra do Dande, Angola.

DESCRIPTION. The single specimen from Barra do Dande consists of a straight arm 57 mm. long, followed by a complete U-bend and a short portion of the next larger straight arm 11 mm. long. The whorl section is nearly circular throughout, being 6·5 mm. diameter at the smaller end and 9 mm. × 10 mm. at the larger end. The two arms are close together, the maximum width of the gap between them near the hook being only 1 mm. The ribs are relatively widely spaced and are broad and flattened on the internal mould. On the side of the whorl they are inclined slightly forwards towards the venter, which they cross unchanged, but the dorsum is smooth or is crossed by striae only. Immediately before the hook there is a constriction preceded by a collar on the venter. On the hook the ribs are smaller and more striate, and just beyond the hook there is a second constriction on the short portion of the larger arm. No suture-lines are visible on this specimen.

The other specimens are all fragments of straight arms up to 50 mm. long and have dimensions similar to the single specimen described above. All have slightly oblique broad ribs, and two of them have shallow constrictions between two adjacent ribs. Septal surfaces and fragments of suture-lines are present in several specimens.

REMARKS. Spath (1953: 49, 50) determined the Barra do Dande specimen as *Phylloptychoceras* sp. nov. and the Egito specimens as *Polyptychoceras* cf. *pseudogaultianum* (Yokoyama). However, all are clearly conspecific and are referred here to Yokoyama's species, from which they show no significant differences. Yokoyama (1890: pl. 20, figs. 1–3) figured three syntypes, the two largest (figs. 1, 2) being comparable in size with the Angolan specimen and showing the same type of ribs, while the smallest (fig. 3) is more densely ribbed and has occasional constrictions. Wiedmann (1962: 185) referred this fine-ribbed syntype to the north German Upper Santonian and Campanian species *P.* (?) *obliquecostatum* (Schlüter). Whether this is correct or whether the specimen falls within the variation of *P. pseudogaultianum* must await the analysis of a larger Japanese topotype collection, and also a proper generic assessment of Schlüter's species which is known only from short straight fragments. *P. pseudogaultianum* occurs in both the Santonian and Campanian of Japan. Four other Japanese species, *P. haradanum* (Yokoyama), *P. subquadratum* (Yokoyama), *P. subundulatum* (Yokoyama) and *P. obstrictum* (Jimbo) differ in size and details of ribbing.

P. vancouverense (Whiteaves) (Usher 1952: 101, pl. 26, figs. 5, 6) is a closely related species from the Upper Campanian of British Columbia. It is slightly larger and has more widely spaced, flattened band-like ribs than *P. pseudogaultianum.* The Graham Land specimens described by Spath (1953: 18, pl. 7, fig. 5) as *Polyptychoceras* sp. juv. indet. are indeterminable and could equally well be *Glyptoxoceras* or *Diplomoceras.*

Subptychoceras has ribs arranged in groups on low bulges and *Phylloptychoceras* has undulating folds on the sides of the whorl and some striae; both are best considered subgenera of *Polyptychoceras.* The lectotype of *Phylloptychoceras sipho* (Forbes), the type species of the subgenus, is figured here (Pl. 11, fig. 1) because previous determinations of this species have had to rely on the inadequate drawings of Forbes (1846: 118, pl. 11, figs. 5*a-g*) and Stoliczka (1865: 194, pl. 90, figs. 5–9), and the figure of the suture-line given by Spath (1953: pl. 11, fig. 7).

Family **DESMOCERATIDAE** Zittel 1895

Subfamily **PUZOSIINAE** Spath 1922

Genus ***KITCHINITES*** Spath 1922

Kitchinites angolaensis sp. nov.

Plate 11, figs. 4–6

HOLOTYPE. C. 52675 (Pl. 11, fig. 5), from 1 km. north of Egito, Angola.

MATERIAL. In addition to the holotype, 8 paratypes (C. 52676–83) all from 1 km. north of Egito, Angola.

DIMENSIONS:

C. 52675. At 64 mm.: 28·7, —, 16·5.
C. 52680. At 48·5 mm.: 22·0, —, 11·9.

DIAGNOSIS. Whorls moderately involute, inner whorls about one half concealed. Whorl section compressed, with only slightly convex whorl sides, vertical umbilical walls and an angled umbilical edge. On whorls up to 40 mm. diameter the ornament consists of fine, slightly sigmoidal ribs which curve gently forwards on approaching the venter; primary ribs cross whole side of whorl and intercalated secondaries occur on ventral half only. Between 40 and 50 mm. diameter ribs gradually fade on inner half of whorl leaving ribs near the venter only. At larger sizes ventral ribs show marked increase in strength. 4 to 6 constrictions per whorl are present, but poorly developed; on inner whorls they are of similar shape to the ribs but inclined more strongly forwards and cut across the ribs; at larger sizes they are nearly straight on side of whorl and curve slightly forwards on the venter. On outer surface of shell, constrictions usually represented by or preceded by a collar on the venter. Suture-lines not visible in detail.

REMARKS. These nine specimens were identified by Spath (1951: 8) as "Gen. nov. (*Kitchinites ?*) sp. nov.", but their generic characters are those of *Kitchinites* and there are no adequate reasons for separating them. *K. angolaensis* is characterized by fine sigmoidal ribs at small sizes, followed at larger sizes by smooth whorl sides and considerably stronger ventral ribs. All the specimens are partly crushed making estimation of the whorl thickness difficult. The most closely related species is *K. darwini* (Steinmann 1895: 73, pl. 5, fig. 3) from the Quiriquina Beds of Chile, which has the same smooth whorl sides, but differs in its larger umbilicus, thicker whorls with more convex sides and its much stronger constrictions. The New Zealand species *K. brevicostata* (Marshall 1926: 183, pl. 24, fig. 3, pl. 43, fig. 2) is also close to *K. angolaensis*, but it has a larger umbilicus and nearly straight ribs that do not fade on the side of the whorl. The type species *Kitchinites pondicherryanus* (Kossmat 1897: 40, pl. 6, fig. 6) has much stronger straight ribs throughout and there is no evidence of the ribs fading on the sides of the whorl.

The genus *Neopuzosia* Matsumoto 1954, was proposed for the two Japanese species, *N. japonica* (Spath), the type species, and *N. ishikawai* (Jimbo) (see Matsumoto 1954: 89–95), which have sigmoidal ribs, at least on the inner whorls, that are strongly projected on the venter. The whorl is generally thicker and not so flattened as in *Kitchinites*. *Neopuzosia* is now generally admitted as a subgenus of *Kitchinites*, but *K. brevicostata* mentioned above is intermediate between the two in most of its characters, and now *K. angolaensis* shows mixed rather than intermediate characters. Its sigmoidal and fine ribs are like those of *Neopuzosia*, its compressed and flattened whorls are like those of *Kitchinites*, while its smooth whorl sides at larger sizes are shared only with *K. darwini*, usually placed in *Kitchinites* s.s. *Neopuzosia* is Santonian and Lower Campanian in age, *Kitchinites* s.s. ranges from Campanian to Lower Maastrichtian, and *K. angolaensis* is Upper Campanian. The horizon of *K. darwini* is not accurately known. Proposal of further generic names will confuse what is probably a closely related group of species; *K. angolaensis* is referred here to *Kitchinites* s.l., rather than to either subgenera which are of doubtful value.

Five species of *Kitchinites* s.l. from the Lower Campanian of Madagascar were described by Collignon (1961: 55–58). All of them have considerably thicker whorls than any of those listed above, but from their convex whorl sides and ribs projected on the venter they would probably be referred to *Neopuzosia* rather than to *Kitchinites* s.s. Of Collignon's five specific names, *K. busnardoi*, *K. quadratus* and *K. fascigerus* (Collignon 1961: pl. 6, figs. 3, 4, pl. 23, fig. 3) represent a species with coarse ribs, while *K. flabelliformis* and *K. enayi* (Collignon 1961: pl. 6, fig. 5, pl. 23, fig. 2) represent a species with much finer ribbing. The ornament of the latter species is hardly distinguishable from that of *K. angolaensis*, but the whorl thickness of the Madagascan species must be about twice that of the Angolan species, even allowing for the crushing in the latter. The Upper Turonian "*Neopuzosia*" *matsumotoi* figured by Collignon (1961: 54, pl. 23, fig. 1) appears to be a *Mesopuzosia* close to the holotype of *M. pacifica* Matsumoto (1954: 82, pl. 15, fig. 1).

Subfamily **DESMOCERATINAE** Zittel 1895

Genus ***DESMOPHYLLITES*** Spath 1929

Desmophyllites diphylloides (Forbes)

Plate 11, fig. 3

1846 *Ammonites diphylloides* Forbes: 105, pl. 8, fig. 8.
1953 *Desmophyllites diphylloides* (Forbes); Spath: 21, 49, pl. 2, figs. 5, 6.
1955 *Desmophyllites diphylloides* (Forbes); Matsumoto & Obata: 121, pl. 24, figs. 1–5, pl. 30, fig. 1.
1959*b* *Desmophyllites diphylloides* (Forbes); Matsumoto: 9, pl. 3, fig. 3.
1961 *Desmophyllites diphylloides* (Forbes); Collignon: 61–65, pl. 24, figs. 4, 5, pl. 25, figs. 1–8.

MATERIAL. 8 specimens, C. 41475 and C. 52661–67, from 1 km. north of Egito, Angola.

DESCRIPTION. The eight specimens vary in size from 20 to 39 mm. diameter and all are wholly septate, but only three are well preserved and free from lateral crushing. Dimensions of these three are as follows:

C. 41473. At 30 mm.: 16·5, 12·5, 2·4.
C. 52663. At 28·5 mm.: 15·0, 11·8, 2·5.
C. 52664. At 20 mm.: 10·7, 8·3, —.

All the specimens are unornamented except for constrictions on the internal mould which are biconcave forwards on the sides of the whorl and are projected forwards on the venter. There are 6 or 7 constrictions per whorl.

REMARKS. Full synonymy and description of this species have been given by Matsumoto & Obata (1955), Matsumoto (1959b) and Collignon (1961). The best of the Angolan specimens and the largest of Forbes's three paratypes were figured by Spath (1953, pl. 2, figs. 5, 6), and the lectotype is now figured (Pl. 11, fig. 3) for the first time since Forbes's original drawing. *D. diphylloides* shows a considerable amount of variation in whorl dimensions, and strength and shape of the constrictions. Collignon (1961: 61—65) has expressed this variation by dividing the Madagascan specimens into four varieties; var. *besairiei* differs from the normal variety in having the constrictions prolonged into a long narrow rostrum on the venter, var. *inermis* has greatly reduced constrictions which are sometimes almost absent, and var. *lata* has a more compressed whorl shape, of which the dimensions listed by Collignon (1961: 64) fall just below the lower limit of the species indicated on the whorl height/breadth graph of Matsumoto & Obata (1955: 124). Undoubtedly these varieties express the normal amount of variation that is now held to occur in many species of ammonites. The Angolan specimens show about average characters of the species and would be referred to the normal variety.

The species has a world-wide distribution in India, Japan, western north America, Angola, Madagascar and south-east Africa. It has a relatively long range for an ammonite species, which Matsumoto (1959*b*: 11; 1959*c*: 70) gave as the whole of the Campanian in Japan and extending up into the Lower Maastrichtian in some other areas. Collignon (1961: 61–65), however, recorded many of his specimens from both Lower and Upper Santonian, and it seems that a range from Lower Santonian to Lower Maastrichtian must be admitted.

Subfamily **HAUERICERATINAE** Matsumoto 1938

Genus ***OIOPHYLLITES*** Spath 1953

Oiophyllites angolaensis Spath

1953 *Oiophyllites angolaensis* Spath: 21, pl. 6, fig. 6.

HOLOTYPE. C. 41476, the only specimen, from 1 km. north of Egito, Angola.

REMARKS. The holotype of this species has been adequately figured by Spath (1953: pl. 6, fig. 6), and consists of wholly septate and somewhat eroded inner whorls of 22 mm. maximum diameter. No part of the shell is preserved and the surface of the internal mould shows no trace of ornament. The whorl section is elliptical with the greatest width near the umbilical edge, and the venter is smoothly rounded with no keel, although this does not exclude the possibility of a keel occurring at this size on the external surface of the shell. Dimensions: at 22 mm.: 10·0, 6·2, 5·7.

This specimen was referred to *Oiophyllites* because of its resemblance to the five Graham Land specimens of *O. decipiens* Spath (1953: 21, pl. 4, figs. 7, 8), the only other species of the genus. The Graham Land specimens are even more poorly preserved, but the shell is present in some places and shows that there is no keel on the shell at 22 mm. diameter, and that sigmoidal striae cover the surface of the shell. There are no constrictions. Matsumoto & Obata (1955: 136–137, text-fig. 6) refigured two of the Graham Land specimens and suggested that the genus was an offshoot of *Hauericeras*, and Collignon (1961: 21) has relegated *Oiophyllites* to a subgenus of *Hauericeras*. The generic status and position of *Oiophyllites* cannot be decided until much larger and better preserved material is available. The single specimen of *O. angolaensis* may be merely the inner whorls of *Hauericeras* as suggested by Matsumoto & Obata (1955: 137), for larger specimens might reveal the presence of a keel at a later growth stage. The Graham Land *Oiophyllites* were associated with a fauna containing *Maorites*, a genus that can be accurately dated as Lower Campanian in Madagascar.

Family **PACHYDISCIDAE** Spath 1922

Genus ***EUPACHYDISCUS*** Spath 1922

Eupachydiscus pseudogrossouvrei Collignon

Plate 12, figs. 1, 4

1931 *Pachydiscus grossouvrei* Kossmat; Basse: 26, pl. 3, figs. 8, 9 (*non* pl. 2, figs. 16, 17).
1932 *Parapachydiscus besairiei* Basse; Collignon: 28, pl. 8, fig. 2.
1955 *Eupachydiscus pseudogrossouvrei* Collignon; 42, pl. 8, figs. 1, 2.

MATERIAL. 7 specimens, C. 52668–74, from 1 km. north of Egito, Angola.

DESCRIPTION. All the specimens are crushed and distorted to some extent, but in places the shell and ornament are well preserved. The largest is 105 mm. diameter and has the best preserved whorl shape with the following approximate dimensions: at 85 mm.: 40 (0·47), 40 (0·47), 20 (0·24). The whorl section is circular with smoothly rounded umbilical walls. The ribs are radial and nearly straight on the sides of the whorl, and curve forwards to form a slight projection on the venter. In most cases long and short ribs alternate, the long ones starting at the umbilical seam and the short ones starting some way up the side of the whorl. There are no tubercles on the ribs at the umbilical edge. The largest specimen has 33 or 34 ribs on its outer whorl at 105 mm. maximum diameter. Septa and suture-lines are poorly preserved and are only seen in a few places, and the largest specimen is septate at its maximum size.

REMARKS. Spath (1951: 8; 1953: 49) determined these specimens as "*Eupachydiscus* sp. (cf. *haradai*, Jimbo sp.)". *E. haradai* (Jimbo) has been described at length by Matsumoto (1954*a*: 281–287, pl. 8, fig. 2, pl. 9, pl. 10, figs. 1–3; 1959*b*: 33–38) from the Japanese type material and examples from California and Canada, and some of the Canadian examples were separated as a slightly more compressed subspecies. Madagascan specimens of *E. haradai* have been figured by Collignon (1938: 78, pl. 4, fig. 4; 1955: 44, pl. 9, fig. 1). All these examples differ from the Angolan specimens in having thicker whorls, stronger ribs surmounted by tubercles at the umbilical edge, and a constriction-like depression associated with some of the major ribs. The Angolan specimens have straighter and less strong ribs and no tubercles or constrictions, and they agree exactly with the species *E. pseudogrossouvrei* from Madagascar. The age of this species is known to be the upper part of the Middle Campanian in Madagascar (Collignon 1955: 88–89; Besairie & Collignon 1960: 77–78). Another Madagascan specimen was separated by Collignon (1955: 43, pl. 8, fig. 2) as var. *undulatocostata* on account of its slightly closer and gently curved ribs. The single specimen on which this variety was founded occurs somewhat lower in the Middle Campanian than the normal form, and if it is genuinely separable, then the Angolan specimens agree with the normal variety with straight ribs.

Most other species of *Eupachydiscus* (for lists see Collignon 1955: 79) have tubercles or bullae at the umbilical edge and stronger and more widely spaced ribs, and the only one which is close to *E. pseudogrossouvrei* is *E. launayi* (Grossouvre 1894: 184, pl. 19). In France *E. launayi* is known only from the single type specimen from the Lower Campanian, but 15–20 specimens have been described by Collignon (1938: 60, pl. 1, fig. 2; 1955: 36–38, pl. 5, fig. 1) from the Lower Campanian of Madagascar, well below *E. pseudogrossouvrei* in the Middle Campanian (Collignon 1955: 89; Besairie & Collignon 1960: 78). *E. launayi* differs from *E. pseudogrossouvrei* only marginally in having slightly higher and thicker whorls and feeble tubercles on the ribs at the umbilical edge. Specimens very close to *E. launayi* were described by Collignon (1955: 39, pl. 6, fig. 2) from a higher level in Madagascar and overlapping with the horizon of *E. pseudogrossouvrei*. The ribs in this form are more dense, the tubercles are larger and the periodic larger ribs appear at an earlier stage than in *E. launayi*, so its resemblance to *E. pseudogrossouvrei* is less close.

Family **PLACENTICERATIDAE** Hyatt 1900

Genus ***HOPLITOPLACENTICERAS*** Paulcke 1906

TYPE SPECIES. *Hoplites plasticus* Paulcke 1906 (ICZN Opinion 554); the lectotype of the species is Paulcke 1906, pl. 13, figs. 1, 1*a-d*.

The specific classification of *Hoplitoplacenticeras* is in a state of confusion owing to the apparently large amount of variation in a single species, and the nine rather poorly preserved Angolan specimens do not clarify any of the difficulties. *Hoplitoplacenticeras* is, however, one of the most important genera for dating the beds at Egito, and it will be useful to outline the basis on which this genus has been accurately dated.

Evidence relating to the position of *Hoplitoplacenticeras* in the classical sections of France and Germany was summarized by Grossouvre (1901: 801–803, table 35), who found that with the exception of *H. lafresnayanum* (d'Orbigny) (known from only one, or perhaps a very few, specimens from the Calcaire à *Baculites* of Manche that contains other ammonites characteristic of the Neubergicus Zone, Lower Maastrichtian), all the other species of the genus characterize a zone at the top of the Campanian, which was named after the most typical species, *H. vari* (Schlüter). More recent work by Jeletzky (1951: 18, 74) has shown that the Upper Campanian is divisible into two zones, of which the lower one is the zone of *H. vari* and contains all the species of *Hoplitoplacenticeras*.

Besairie & Collignon (1960: 74–80) have summarized the accurate stratigraphical work of Hourcq (1950: 64–85) and earlier workers in Madagascar and have shown that the few specimens of *Hoplitoplacenticeras* in that island are confined to the *H. vari* Zone, taken there as comprising the whole of the Upper Campanian. Direct evidence as to the age of the *H. plasticum* fauna in Patagonia is poor, for the only associated forms at the same locality, Cerro Cazador f (Paulcke 1906: 235–240), are several long-ranging species of Tetragonitidae, and *Pseudokossmaticeras paulcki* Collignon (1955*a*: 44) which might be of Upper Campanian age, although most species of the genus are Maastrichtian. *Hoplitoplacenticeras vancouverense* occurs in the Cedar District Formation in British Columbia, which can be dated fairly accurately as Upper Campanian (Usher 1952: 38–39). A specimen of *Hoplitoplacenticeras* found in Wyoming (Cobban 1963: C60) has allowed one point in the established zonal sequence of baculitids in the western interior of the United States to be correlated against the standard Campanian sequence of Europe.

Hoplitoplacenticeras cf. *marroti* (Coquand)

Plate 12, fig. 3, Pl. 13, fig. 3

1859 *Ammonites marroti* Coquand; 995.
Cf. 1867 *Ammonites coesfieldensis* Schlüter: 14, pl. 1, figs. 2, 3, 5, *non* figs. 1, 4.
Cf. 1867 *Ammonites costulosus* Schlüter: 17, pl. 2, fig. 1, *non* figs. 2–4.
Cf. 1872 *Ammonites striatocostatus* Schlüter: 65, pl. 20, figs. 1–4.
Cf. 1872*a* *Ammonites vari* Schlüter: 92.

Cf. 1876 *Ammonites vari* Schlüter; Schlüter: 160.
1894 *Ammonites vari* Schlüter var. *marroti* Coquand; Grossouvre: 118, pl. 8, fig. 3, pl. 9, figs. 2, 3.
1898 *Hoplites vari* var. *marroti* (Coquand); Choffat: 80, pl. 20, figs. 1–5.
Cf. 1906 *Hoplitoplacenticeras plasticum costatum* Paulcke: 34, pl. 11, fig. 2, pl. 12, figs. 1–3, ? pl. 13, fig. 2.
1925 *Hoplitoplacenticeras vari* (Schlüter); Diener: 178.
1929 *Hoplites* cf. *vari* (Schlüter); Barrabé: 181, pl. 9, figs. 11–13.
? 1931 *Hoplites vari* (Schlüter); Basse: 35, pl. 5, figs. 1–3, pl. 12, fig. 2, pl. 13, fig. 1.
1947 *Hoplitoplacenticeras vari* (Schlüter); Chavan: 129, pl. 2, fig. 1.
1963 *Hoplitoplacenticeras marroti* (Coquand) Young: 63, pl. 2, figs. 5, 15, 17, pl. 17, figs. 3, 4, pl. 20, figs. 2, 3, pl. 21, figs. 1, 4, pl. 81, fig. 4.

MATERIAL. Two specimens, C.52684–85, from 1 km. north of Egito, Angola.

DESCRIPTION. Both specimens consist of about half a single whorl, roughly 60 mm. and 45 mm. diameter, which are rather poorly preserved and slightly distorted. The whorl breadth is about two-thirds of the height and the whorl section is angled at the tubercles. Long, slightly sigmoidal primary ribs alternate with less prominent secondary ribs which commence at the middle of the side of the whorl. The ribs cross the venter but are much reduced between the ventral tubercles. There are small umbilical tubercles, small mid-lateral tubercles, moderate, clavate lower ventro-lateral tubercles, and small upper ventro-lateral tubercles.

REMARKS. The holotype of *H. marroti* was figured by Grossouvre (1894, pl. 8, fig. 3), and this specific name has priority over *H. vari* Schlüter (1872*a*) which was substituted by Schlüter for his *Ammonites striatocostatus* Schlüter (1872:65) already preoccupied by Meneghini (1856). The type specimens of *H. vari* are therefore those described and figured by Schlüter (1872: 65, pl. 20, figs. 1–4.) Other specimens referred to *H. vari* by Schlüter are those listed as *Ammonites coesfieldensis* and *A. costulosus* in the synonymy above, but the proper interpretation of *H. vari* must await a full revision of Schlüter's types and further topotype material. Judging from the best of Schlüter's figured specimens (1872, pl. 20, figs. 1, 2), *H. vari* is probably conspecific with *H. marroti*, but it may be found that a varietal distinction, *H. marroti* var. *vari*, is necessary. *H. praematura* (Imkeller 1901: 58, fig. 1) from the northern Alps may be another variety of *H. marroti*, but from its apparently early loss of tubercles full specific distinction may be advisable.

The two Angolan specimens agree well with the holotype of *H. marroti*, although they differ in the development of a small mid-lateral tubercle, and the lower ventro-lateral tubercle is as large as, or larger than, the upper ventro-lateral tubercle. Their fragmentary nature and preservation does not allow further comparisons to be made. The Portuguese examples figured by Choffat, the Madagascan examples figured by Barrabé, the Palestine example figured by Chavan and the Texas examples figured by Young, all listed in the synonymy above, conform more-or-less closely with *H. marroti*. Further Madagascan examples figured by Basse (1931: 35, pl. 5, figs. 1–3) are more compressed and have less prominent ribs. The other European species of *Hoplitoplacenticeras* differ markedly: *H. dolbergense* (Schlüter 1876: 159, pl. 44, figs. 1–4) is the closest, but its ventro-lateral tubercles are larger and the ribs are looped to them; *H. coesfieldensis* (Schlüter 1867: 14, pl. 1, figs. 1, 4 only), and *H. lemfordense* (Schlüter 1876: 160, pl. 44, figs. 8, 9) have dense, well marked ribs; and *H. lafresnayanum* (d'Orbigny 1842: 326, pl. 97, figs. 3–5; Grossouvre 1894, pl. 23, fig. 4) is a Lower Maastrichtian species that has bold and strongly inclined ribs. Amongst the Patagonian forms of *H. plasticum*, *H. plasticum costatum* Paulcke (see synonymy) agrees with the Angolan specimens in strength of ribs and tubercles, but its ribs are almost straight, not sigmoidal.

Hoplitoplacenticeras cf. ***costulosum*** (Schlüter)

Plate 13, fig. 2

1867 *Ammonites costulosus* Schlüter: 17, pl. 2, figs. 2–4, *non* fig. 1.
1872 *Ammonites costulosus* Schlüter; Schlüter: 66, pl. 20, figs. 5, 6.
1906 *Hoplitoplacenticeras plasticum laeve* Paulcke: 45, pl. 14, figs. 3, 4, pl. 15, figs. 2, 3.
1931 *Hoplites* (*Hoplitoplacenticeras*) *plasticum* Paulcke; Basse: 36, pl. 4, figs. 5, 6, pl. 12, fig. 3.

MATERIAL. Three specimens, C.52686–88, from 1 km. north of Egito, Angola.

DESCRIPTION. The three specimens are 32 mm., 27 mm. and 22 mm. diameter respectively, and the outer whorl of the largest is fairly well preserved. The whorl shape is compressed, with almost flat whorl sides tapering towards a narrow flat venter. The sigmoidal ribs are of low relief, but are broad and flat, and the interspaces are narrow. The umbilical tubercles are only small raised portions of the ribs. The lower ventro-lateral tubercles are clavate ends to the ribs, and the upper ventro-lateral tubercles are smaller and are situated on the venter. There are no mid-lateral tubercles.

REMARKS. The largest Angolan specimen compares well with the most strongly ribbed of those figured by Schlüter (1867, pl. 2, fig. 2) and with the smoothest specimen figured by Paulcke (1906 pl. 15, fig. 2), except that both Schlüter's and Paulcke's figures show only one ventro-lateral tubercle, while the Angolan specimens have both upper and lower ventro-lateral tubercles close together. Schlüter (1867, pl. 2, figs. 3, 4) also figured specimens in which the ribs are striate, and Paulcke (1906, pl. 15, fig. 3) figured one which develops prominent umbilical tubercles. The relationship of Schlüter's and Paulcke's species cannot be deduced until their respective ranges of variation are worked out, and further specimens figured photographically to show the type of ventro-lateral tubercles developed. Two Madagascan specimens figured by Basse (1931, pl. 4, figs. 5, 6) are similar to the Angolan specimens. *H. vancouverense* (Meek 1976*a*: 370, pl. 6, fig. 1; Usher 1952: 93, pl. 25, figs. 1, 2) also has reduced ribs at all growth stages, but it differs in its thicker whorls and much larger vertro-lateral tubercles. *H. lafresnayanum* (d'Orbigny) (Grossouvre: 1894: 121, pl. 23, fig. 4) has a similar pattern of tubercles, but it has considerably stronger ribs.

Hoplitoplacenticeras spp. indet.

MATERIAL. Four specimens, C.52689–92, from 1 km. north of Egito, Angola.

Description. Three of the specimens (C.52689–91) are the inner whorls of an indeterminate species of this genus. The fourth specimen (C.52692) differs markedly from any hitherto described species. It is 26 mm. diameter and the preservation is sufficiently good to see that the whorl is very broad, with a height to breadth ratio of about 0·7, there are large tubercles or spines on the side of the whorl, and the wide, flat venter has four rows of small tubercles, the inner pair of rows bounding a well marked mid-ventral groove. The pattern of tubercles is similar to that of one of Paulcke's specimens (1906, pl. 13, fig. 2), but the wide, flat, centrally grooved venter is more exaggerated and the maximum size of the specimen is only 26 mm. diameter.

Family **SPHENODISCIDAE** Hyatt 1900

The type of subdivision of the first lateral saddle of the suture-line has been regarded by most workers as the most important generic character in this family. A primary bifurcation of the first lateral saddle has always been taken as distinctly different from a primary trifurcation of the saddle. Within the two groups thus formed genera have been separated according to the degree of indentation of the saddles and to major differences in ornament and whorl shape. The nomenclature is complicated by a considerable number of ammonites having a primary bifurcation of the first lateral saddle followed by another bifurcation of the ventral half of the saddle, the resulting pattern of "secondary trifurcation" remaining clear throughout growth. Such forms have been variously referred to the nearest existing genera or made the basis of new generic names. The classifications adopted by Picard (1929: 452–453), Olsson (1944: 108–112), Hourcq (1949: 113–115) and Basse (1954: 866–869) were based on these lines, where primary consideration was given to the subdivision of the first lateral saddle.

Wright (1957: *L*437) was the first to point out that details of suture-lines can be misleading in this family, and the classification which he adopted showed a more balanced appraisal of all the characters. With the discovery of the Angolan specimens described below which appeared to be typical *Manambolites*, except that the first lateral saddle showed primary trifurcation, not bifurcation, the possibility that this character was not of generic value, and perhaps not even of specific value, required investigation. The characters of the species referred to all the sphenodiscid genera can be summarized as follows (see Wright 1957: *L*437 for details of nomenclature):

1. *Libycoceras* Hyatt 1900. All saddles entire. First lateral saddle shows either bifurcation or secondary trifurcation. All species are ornamented, except *L. acutodorsatum* and the unfigured and undescribed species *L. chargense* Blanckenhorn (1900: 45) which are smooth. The species showing secondary trifurcation is *L. acutodorsatum* (Noetling 1897: 76, pl. 21, fig. 3) which has always been referred before to *Sphenodiscus*, but all its saddles are entire, wholly unlike even the simplest suture-line of *Sphenodiscus*. *Paciceras* Olsson (1944: 110–112) is a synonym, and it shows the beginnings of a secondary bifurcation of the outer half of the bifid first lateral saddle.

2. *Indoceras* Noetling 1897. Like *Libycoceras*, with first lateral saddle bifid, but smooth and with rounded venter at least on the two outer whorls.

3. *Manambolites* Hourcq 1949. All parts of the first lateral saddle are indented and sometimes the second lateral saddle also. Remaining saddles entire. First lateral saddles either bifid or trifid, and some bifid examples have a tendency to a second bifurcation of the outer half. Smooth or feebly ornamented. The trifid species is the Angolan form described below. A considerable amount of variation in suture-line details was shown to exist by Hourcq (1949: 112, figs. 21, 22). *Mzezzemceras* Basse (1954: 868, pl. 17, fig. 2) is a synonym.

4. *Coahuilites* Böse 1927. Suture-lines generally like those of the simpler ones of *Sphenodiscus* and show the same narrow-necked, kidney shaped saddles. Of the three species described by Böse (1927: 279–293), the type species has a bifid first lateral saddle, while in the other two species this saddle is bifid then the outer half is bifid again. It differs from *Sphenodiscus* by its well marked ribs and tubercles, and rounded or flat venter at some stage. *Daradiceras* Sornay & Tessier 1949, is an extreme development of *Coahuilites* showing large ribs and tubercles, and might be considered a subgenus of *Coahuilites*.

5. *Sphenodiscus* Meek 1871. All saddles of the suture-line usually indented, but some or all of the auxiliary saddles may be entire. Saddles narrow-necked and kidney shaped in complicated suture-lines. First lateral saddle usually trifid, but examples are known where this saddle is primarily bifid, with the outer half bifid again. One series of such examples were made the basis of the genus *Austrosphenodiscus* Olsson (1944: 108–110), and the Texan species *S. pleurisepta* (Conrad) has a suture-line in which the range of variation includes both trifid and bifid examples—the suture-line of an example which is clearly bifid, with the outer half again bifid, is shown in Text-fig. 22. Smooth or only weakly ornamented.

The alternative to admitting this amount of variation in the suture-lines of sphenodiscid genera is the further multiplication of generic names by creating new genera for *Libycoceras acutodorsatum* and the Angolan species described below, according generic status to *Austrosphenodiscus*, and possibly creating a new genus or subgenus for the specimen of *S. pleurisepta* referred to above. Such a purely morphological classification would obscure relationships, and tend to separate into different genera even conspecific specimens.

The age of spenodiscid genera by dating against associated ammonites of zonal value is not as well established as is often assumed, for the mere presence of any sphenodiscid has too often been taken as an indication of a Maastrichtian age. The type species of *Manambolites* occurs in the Middle Campanian in Madagascar and at one locality it occurs as low as the base of the Middle Campanian (Hourcq 1949: 113; Besairie & Collignon 1960: 77–79). The other species of *Manambolites* are probably Upper Campanian only. Evidence that the type species of *Libycoceras* and the associated *L. chargense* Blanckenhorn are Upper Campanian in age in north Africa and the Middle East was presented by Reiss (1962); they occur in the Zone of *Bostrychoceras polyplocum*, taken as the top of the Upper Campanian. No other species of *Libycoceras* (including *Paciceras*) are accurately dated. *Indoceras* is not accurately dated against associated ammonites. The earliest species of *Coahuilites* are probably Upper Campanian, but later ones are undoubtedly Maastrichtian. *Sphenodiscus* is well dated at many localities as Maastrichtian (see pp. 403-404), and it is not known in the Upper Campanian. In the present state of knowledge derivation of the whole family from *Eulophoceras* at the end of the Lower Campanian is the most likely phylogeny.

Genus ***MANAMBOLITES*** Hourcq 1949

Manambolites dandensis sp. nov.

Plate 12, fig. 2, Pl. 13, fig. 1; Text-figs. 18–21

1953 Gen. nov. ("*Sphenodiscus*") sp. nov. aff. *Manambolites spathi*, Picard sp.; Spath: 49, pl. 3, fig. 6.

HOLOTYPE. C. 41474 (Pl. 13, fig. 1), from Barra do Dande, Angola.

MATERIAL. In addition to the holotype, C. 52734, C. 52736 (paratypes), and C. 52735, from Barra do Dande, Angola.

DIAGNOSIS. Smooth or very feebly ornamented species, of which the first lateral saddle of the suture-line is divided into three by two adventitious lobes. The three parts of the first lateral saddle are slightly indented, all other saddles entire.

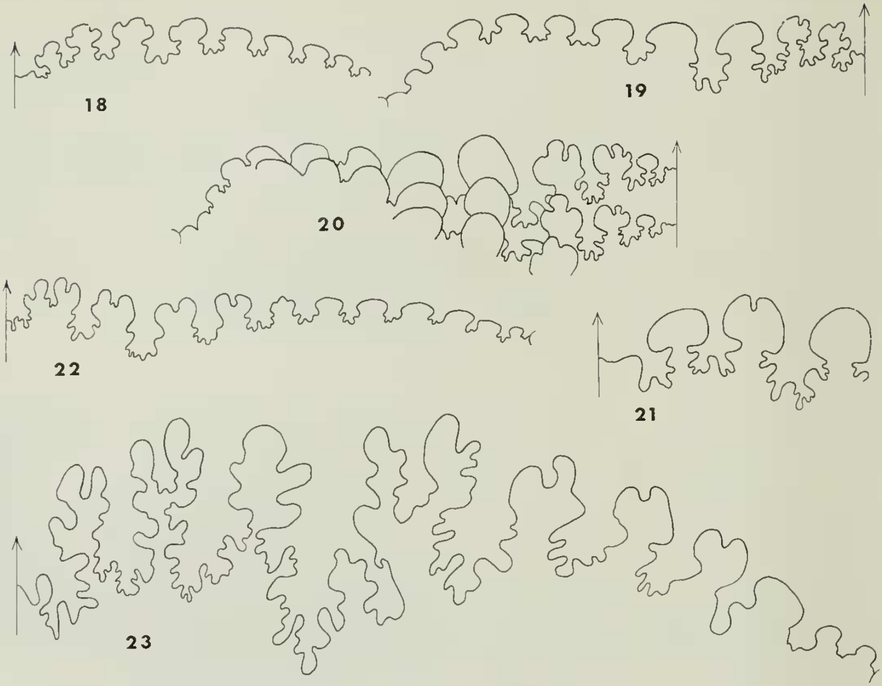
DESCRIPTION. The holotype is an adult specimen measuring 134 mm. diameter at the nearly complete mouth border. The adult body chamber occupies slightly less than half a whorl and has extensively modified features. The whorl height is markedly lowered away from the true spiral; from the beginning of the body chamber the venter alters rapidly from sharp to evenly rounded, and near the mouth border becomes almost tabulate; and near the mouth border the thickness of the dorsal half of the whorl is greatly contracted. The mouth border curves gently forwards on approaching the venter, but no part of it is preserved on the venter itself. The half whorl before the body chamber is preserved complete with the shell; the umbilicus is a pin hole, the whorl shape is oxycone with a sharp venter, and the evenly convex sides of the whorl are interrupted just before the venter by a slight rounded ridge. Sinuous growth striae cover the shell surface, and there are very low radial undulations on the outer half of the whorl side which reach as far as the low spiral ridge; at the middle of the side of the whorl there are very small radially elongated raised portions on each undulation. The final suture-line is completely exposed together with parts of the two previous ones, and these appear to be crowded though they cannot be compared with earlier ones. The first lateral saddle is divided into three by two adventitious lobes, the outer lobe is smaller than the inner one but the saddle as a whole is clearly trifid rather than bifid, and the three saddles thus formed are moderately indented. The second lateral saddle and the seven auxiliary saddles are entire. The last three auxiliary saddles just before the umbilicus are markedly retracted.

The two paratypes are wholly septate specimens. The larger one (Pl. 12, fig. 2) has a maximum diameter of 75 mm., and at this size the last three suture-lines are approximated. This is considerably smaller than the 102 mm. diameter at which the final suture-lines occur in the holotype. This specimen has very low and rudimentary tubercles at the middle of the whorl side from which equally low undulations run to a very slight ridge at the side of the venter. The venter itself is sharpened to a knife edge. The smaller paratype consists of only one-third of a whorl of about 50 mm. diameter. In both paratypes the suture-lines (Text-figs. 18, 19) have the same basic pattern as in the holotype, and in the earliest suture-line visible in the smaller paratype at 38 mm. diameter, the first lateral saddle is clearly trifid. In almost every case the three parts of the first lateral saddle are indented, and all the other saddles are entire.

REMARKS. Three of the specimens described here formed the basis of Spath's (1951: 9, 1953: 49) three determinations—"*Manambolites* sp. nov. aff. *M. spathi* (Picard)" (also "Gen. nov. ("*Spenodiscus*") sp. nov." in 1953: 49, pl. 3, fig. 6), "*Libycoceras angolaense* Haughton" and "*Libycoceras* sp. nov.". There is a fourth specimen in the collection, C. 52735, which is a fragment of part of a whorl of roughly 120 mm. diameter, and has the ventral parts of six suture-lines (Text-fig. 21). The last three of these are noticeably closer together and they may be the adult suture-lines. Those parts of the suture-line that can be seen agree with the present species, but the specimen is broken before the first lateral saddle is reached in each case, so the specimen can only be identified as *Manambolites* cf. *dandensis*.

The most closely comparable species is *Manambolites piveteaui* Hourcq (1949: 111, pl. 3, fig. 1) from Madagascar, which has the same adult body chamber modifications, but differs in its clearly bifid first lateral saddle. The suture-line of this species shows considerable variation in details as can be seen from Hourcq's figures (1949: 112, figs. 21, 22), but the basic pattern of a first lateral saddle is constant. It is from the Middle Campanian of Madagascar (Besairie & Collignon 1960: 77–79). The only other described species of *Manambolites* are *M. spathi* (Picard 1929: 449, fig. 10) from the Upper Campanian of Palestine, which has the characteristic suture-line with a bifid first lateral saddle, but is otherwise poorly preserved, and *M. pervinquieri* (Basse 1954: 866, pl. 17, fig. 2) from Tunisia (probably from the Upper Campanian), which is very close to *M. piveteaui*, has the same bifid first lateral saddle, but may have slightly stronger ornament. *M. pervinquieri* was made the type species of *Mzezzemceras* Basse (1954: 868) used as a subgenus of *Coahuilites*, but its relationships to *Manambolites* are so close (it may even be conspecific with *M. piveteaui*, the type species of the genus) that it must be considered a synonym of that genus.

"*Manambolites*" *ricensis* Young (1963: 127, figs. 8*f*, 9*m*, *p*, 11*h*, pl. 2, figs. 14, 16, 19, pl. 72, fig. 4, pl. 74, fig. 2) is, as was pointed out by its author, an enigma. It is undoubtedly from the top of the Campanian in Texas, but it has a suture-line like *Paralenticeras* or *Eulophoceras*. The trifid first lateral saddle and bifid second lateral saddle, of which all parts are well frilled (Young 1963: figs. 8*f*, 9*m*), are distinctly like those of *Paralenticeras* of the Upper Coniacian and Lower Santonian, and resemble to some extent those of *Eulophoceras* which ranges as high as the Lower Campanian,



Figs. 18–23. Suture-lines of Sphenodiscidae. 18–21. *Manambolites dandensis* sp. nov. Upper Campanian, Barra do Dande, Angola. Fig. 18, Paratype, C. 52736, at 26 mm. whorl height, ×2. Fig. 19, Paratype, C. 52734, at 42 mm. whorl height, ×1·6. Fig. 20, Holotype, C. 41474, last suture-lines at 63 mm. whorl height, ×1·1. Fig. 21, First lateral saddle of C. 52735, at approx. 75 mm. whorl height, ×1·5. Fig. 22. *Sphenodiscus pleurisepta* (Conrad). Maastrichtian, Upper Escondido Formation, Honda Creek—Rock Crossing, Medina County, Texas. C. 53965, at 68 mm. whorl height, ×1. Fig. 23. *Sphenodiscus* sp. indet. Maastrichtian, Barra do Dande, Angola. C. 52733, at 108 mm. whorl height. ×1·1.

The most complicated suture-line of *Manambolites* (Hourcq 1949: 112, fig. 22–7) is considerably different.

The only Sphenodiscid ammonites previously recorded from Angola are the three specimens of *Libycoceras angolaense* Haughton (1925: 269–270, pl. 14, figs. 1–5). These have bifid first lateral saddles in every case, all their saddles are entire, and their ornament is characteristic of the genus *Libycoceras*.

Genus ***SPHENODISCUS*** Meek 1871

Sphenodiscus sp. indet.

Text-fig. 23

Material. One specimen, C. 52733, from Barra do Dande, Angola.

Remarks. The specimen is an internal mould and consists of one quarter of a wholly septate whorl preserved on one side only. Its maximum whorl height is

125 mm., which indicates a diameter of about 200 mm. The whorl section is oxycone and highly compressed, and there is no ornament on the internal mould. The suture-line (Text-fig. 23) has a trifid first lateral saddle, and greatly indented parts to the first and second lateral saddles. There are six auxiliary saddles of which the three ventral ones are slightly indented.

Few species of *Sphenodiscus* have suture-lines as complicated as that of the present fragment. The large specimen of *S. lobatus* (Tuomey) figured by Hyatt (1903: 66, pl. 7) is closely comparable in most characters, but its whorl section is much less compressed and its saddle endings differ in detail. Several other north American specimens figured by Hyatt (1903, pl. 6, figs. 3, 4, pl. 8, figs. 3–7, pl. 9, figs. 7–10) differ only in details of the saddle indentations and their number of auxiliary saddles. The suture-line of *S. siva* (Forbes 1846: 110, pl. 7, fig. 6; Stoliczka 1865: 59, pl. 33, fig. 3; Kossmat 1895: 177, pl. 22, fig. 2) is very complicated at the largest known diameter of 65 mm., and larger specimens of this species might be closely comparable with the Angolan specimen.

Family **NAUTILIDAE** d'Orbigny 1840

Genus ***EUTREPHOCERAS*** Hyatt 1894

Eutrephoceras simile Spath

1909 *Nautilus blanfordianus* Kilian & Reboul: 8, pl. 1, figs. 1, 2.
1953 *Eutrephoceras simile* Spath: 40, pl. 12, fig. 4, pl. 13, figs. 1–5, 7.
1956 *Eutrephoceras egitoense* Miller & Carpenter: 34, pl. 1, figs. 1–4.

MATERIAL. Nine specimens, C. 41480 and C. 52710–17, from 1 km. north of Egito, Angola.

REMARKS. Sixteen specimens from the same horizon and locality as the present collection were described as *E. egitoense* by Miller & Carpenter (1956: 34, pl. 1, figs. 1–4). One specimen from the present collection (C. 41480) was figured as *E.* aff. *simile* by Spath (1953, pl. 13, fig. 7). From Miller & Carpenter's description and figures, and from a comparison of the new Angolan material with the Graham Land material, it is clear that the Angolan specimens are *E. simile*, and that *E. egitoense* is a synonym. A specimen from Snow Hill Island, Graham Land, obtained after Spath's original description shows the sharp reticulate pattern of transverse and longitudinal striae in the young growth stages (20–30 mm.) much better than in any of the originals available to Spath. The transverse striae have a slight sinus in the middle of the venter. The Angolan specimens do not differ in any way from the Graham Land examples—they have a whorl height/breadth ratio of about 0·70 at 50 mm. diameter, reticulate striae on the inner whorls, an approximately central siphuncle on the inner whorls that becomes more ventral at larger sizes, and a straight, radial external suture-line that is retracted at the edge of the umbilicus, all characters typical of *E. simile*. As with the collection described by Miller & Carpenter (1956) the specimens are rather poorly preserved and distorted, preserved in a light brown calcareous sandstone, and they do not add anything to the description of those authors.

IV AGES OF THE FAUNAS DESCRIBED

(a) *Douvilleiceras* fauna of Dombe Grande.

The nine specimens of *Douvilleiceras mammillatum* (Schlotheim)? var. *aequinodum* (Quenstedt) and *D. orbignyi* Hyatt from Dombe Grande, are all that now remain of more than 50 examples of *Douvilleiceras* collected in 1930 and 1931 by Alexandre Borges from various localities south-west of Benguela. Borges stated (*in litt.* to Spath) that they all came from beds above the *Pholadomya* beds. In fact Borges had searched the *Pholadomya* beds for ammonites for several years and had found none. Recent work on the stratigraphy of the area south-west of Benguela by Neto (1960: 89–99; 1961: 65–77) has confirmed the placing of these *Douvilleiceras* in beds above the *Pholadomya pleuromyaeformis* beds, and in fact a formation characterized by *Nerinea* (and some indeterminate ammonites) and reaching 400 metres in thickness comes between the *Pholadomya* beds below and the "*Acanthoceras*" (i.e. *Douvilleiceras*) beds above. Therefore Choffat's (1888: 20, 71) placing of one of his two specimens of *Douvilleiceras* in the *Pholadomya* beds is probably incorrect (Mouta & O'Donnell 1933: 58–61).

The age of all the *Douvilleiceras* seen so far is Mammillatum Zone, Lower Albian. This, not Upper Albian, is the age of the "*Acanthoceras*" Formation of Neto (1960: 95; 1961: 69, 74).

(b) *Neokentroceras* fauna of Praia do Jombo.

The Jombo beach lies in the Benguela basin just south-west of the mouth of the Hanha (=Cubal) River and 16 km. north-east of Lobito. This is the same locality as that ("shore at landing place near Hanha") from which most of Spath's original *Neokentroceras* came, and the specimens described by Haas (1942) came from a cliff on the bank of the same river near Hanha. Henrique O'Donnell, who collected the present specimens, said (*it litt.* to Spath) that they came from beds in the lower part of the Upper Albian formation. This is the only direct evidence for their stratigraphical position; but combined with the morphological evidence that they are probably an end-form development of *Hysteroceras*, it is fairly certain that their age is low in the Upper Albian. This is the age of the lowest dateable part of the "*Pervinquieria*" Formation of Neto (1960: 95; 1961: 69, 75), and higher parts of this formation which contain the abundant fauna of *Mortoniceras*, *Elobiceras*, *Puzosia* and Hamitidae are higher in the Upper Albian. The Middle Albian is either represented by a disconformity between the "*Acanthoceras*" and "*Pervinquieria*" Formations, or, more likely, is represented by beds in these formations that do not contain ammonites. The full fauna of *Neokentroceras* at Praia do Jombo consists of the following species; *N. curvicornu* Spath, *N. singulare* Haas, *N. subtuberculatum* Spath, *N. trituberculatum* sp. nov., *N. pseudovaricosum* Spath and *N. crassicostatum* sp. nov.

(c) The Egito fauna.

The Senonian outlier from which the Egito fauna came, is in a small bay 1 km. north of Egito. It is exposed for 1200 m. along the shore, but the variable width of the beds never exceeds 300 m. The formation consists of horizontal marly limestones and coarse sandstones with unfossiliferous clays below, and is 40 m. thick. It rests unconformably on Upper Albian beds containing *Stoliczkaia dispar* in the upper part. According to O'Donnell (*in litt.* to Spath) this outlier is the only one that contains ammonites amongst several similar ones (but with more sandstone and conglomerate) that occur between Egito and Lobito. The full cephalopod fauna from Egito is:

Anagaudryceras mikobokense Collignon
Gaudryceras varagurense Kossmat
Didymoceras subtuberculatum sp. nov.
Polyptychoceras pseudogaultianum (Yokoyama)
Kitchinites angolaense sp. nov.
Desmophyllites diphylloides (Forbes)
Oiophyllites angolaense Spath
Eupachydiscus pseudogrossouvrei Collignon
Hoplitoplacenticeras cf. *marroti* (Coquand)
H. cf. *costulosum* (Schlüter)
H. spp. indet.
Eutrephoceras simile Spath
Tetragonites sp. indet.

All the above species except the last one have been described in the systematic part of this paper. *Tetragonites* sp. indet. is represented by only one specimen that is poorly preserved and not specifically determinable. The presence of *Hoplitoplacenticeras* is sufficient to place the fauna in the zone characterized by this genus (*Hoplitoplacenticeras vari* Zone) in the Upper Campanian. If the Zone of *Bostrychoceras polyplocum* is also put into the Upper Campanian (see discussion of Barra do Dande fauna below) rather than in the Maastrichtian, then the Egito fauna is referable to the lower half of the Upper Campanian. This does not clash with Spath's (1951: 8; 1953: 49) dating of the fauna as the "very top of the Campanian", because Spath was following Haug's classification where the Polyplocum Zone was placed as the basal zone of the Maastrichtian. The second view expressed by Spath in the same papers, that the Egito fauna "could equally well be considered to be basal Maastrichtian", reflected his suspicions that *Hoplitoplacenticeras* might not be confined to the zone that it is said to characterize (Spath 1953: 52) and also his desire to lower the base of the Maastrichtian still further so that it included the Vari Zone as well. But Spath's fears that *Hoplitoplacenticeras* might occur outside the Vari Zone in Madagascar are not justified, for apart from the anomalous species *H. lafresnayanum*, the genus is a good zonal indicator (see p. 391 above). Wherever the Campanian—Maastrichtian boundary is placed, the Egito fauna can be definitely referred to the Vari Zone.

No indication was given by O'Donnell that any part of the ammonite fauna was collected from any particular bed at Egito. The fauna can only be considered as a single unit, and none of the ammonites other than *Hoplitoplacenticeras* conflicts with this placing of the assemblage in a single zone—the Vari Zone of the Upper Campanian. *Eupachydiscus pseudogrossouvrei* occurs in the upper half of the Middle

Campanian in Madagascar, in the Zone of *Delawarella subdelawarensis* (Besairie & Collignon 1960: 77). This does not conflict with its presence in the Vari Zone in Angola, especially as *Hoplitoplacenticeras* is not common in Madagascar and its full range there might not yet be known. *Kitchinites angolaense* is not accurately dateable against any other species of the same genus, which are generally of Campanian or Lower Maastrichtian age. *Desmophyllites diphylloides* has a long range from the Lower Santonian to the Lower Maastrichtian, while *Oiophyllites angolaensis* can only be compared with *O. decipiens* which occurs in the Lower and ? Middle Campanian in Antarctica. Of the three lytoceratid species, *Anagaudryceras mikobokense* occurs in the Lower Maastrichtian in Madagascar and the Lower Maastrichtian or top of the Campanian in California, *Gaudryceras varagurense* occurs in the Santonian in India and has been recorded from the Santonian and Campanian of many other localities, and the *Tetragonites* sp. indet. cannot be accurately dated. Such lytoceratids tend to be relatively long ranging and the presence of all three in the Upper Campanian does not clash with any previous records. The two heteromorph ammonites in the Egito fauna cannot be used for accurate dating: *Didymoceras subtuberculatum* is a new species not clearly related to any other species of the genus that occur in the Campanian or Maastrichtian; *Polyptychoceras pseudogaultianum* occurs in the Santonian and Campanian in Japan, and a closely related species occurs in the Upper Campanian of British Columbia.

(d) The Barra do Dande fauna

The Barra do Dande ammonites collected by Henrique O'Donnell and Beeby Thompson consist of the following species:

Neophylloceras ultimum Spath
Baculites sp. indet.
Didymoceras cf. *hornbyense* (Whiteaves)
D. cf. *angolaense* (Haughton)
Nostoceras hyatti Stephenson
N. cf. *kernense* (Anderson)
N. rotundum sp. nov.
N. helicinum (Shumard)
N. (?) *obtusum* sp. nov.
Solenoceras sp. indet.
Polyptychoceras pseudogaultianum (Yokoyama)
Manambolites dandensis sp. indet.
Sphenodiscus sp. indet.

All the above species, except *Solenoceras* and *Baculites*, have been described in the systematic part of this work. *Solenoceras* is represented by one very small fragment that has fine, slightly oblique ribs and two rows of small tubercles on the venter. It is not worth describing and may belong to either *S. binodosa* (Haughton 1925: 278) or *S. bembense* Haas (1943: 11, figs. 4, 14) from Angola. There is one short indeterminate fragment of *Baculites*.

Spath's first list of the Barra do Dande ammonites (Spath 1951: 9, 10) corresponds exactly with the list given above, but his later list (1953: 49, 50) included in addition all the Angolan Maastrichtian ammonites described by Haughton (1925) and Haas (1943) which came from other localities. Beeby Thompson, whose collection consisted only of six specimens of *Nostoceras hyatti* and one *N. helicinum*, gave no details of the beds at Barra do Dande. Henrique O'Donnell gave the following details (*in litt.*) to Spath: the Senonian at the mouth of the River Dande is about 60 m. thick, and consists of thick beds of more-or-less laminated marls, alternating with thin beds of limestone that are often fossiliferous and typically lenticular with hard crystalline centres; the limestones sometimes contain thin bituminous layers, and the whole series is characterized by the gigantic *Inoceramus langi*. O'Donnell did not indicate that any of his ammonites came from any particular part of the series.

To Beeby Thompson's and O'Donnell's collections must be added the two specimens of *Nostoceras* described by Sornay (1951) and the large *Didymoceras* described by Silva (1961). These three ammonites are definitely recorded as having come from bed 5 of the Barra do Dande section as described by Freneix (1959: 111–113). This is the best and most detailed description of the section, but further details were given by Darteville & Casier (1943: 85–86, fig. 46; 1959: 267–268). Bed 5 is a soft sandy limestone containing a band of black silica and is only 0·30 m. thick; it has been said to be of Campanian age because of the *Nostoceras* it contains. The overlying bed 6, also only 0·30 m. thick, is a gritty limestone containing plant debris, silicified gastropods, coprolites and fish teeth; the latter have been used to date it as Maastrichtian. Bed 7 consists of Recent deposits. The beds below bed 5 account for the remainder of the 60 metres of beds at Barra do Dande, and there is no indication that any of them contained the ammonites collected by O'Donnell. If all the specimens of *Didymoceras* and *Nostoceras* in O'Donnell's collection are considered to come from bed 5, then the matrix of the specimens of *Baculites*, *Solenoceras*, *Polyptychoceras* and *Manambolites* agrees with them exactly—all are preserved in a hard white limestone, with varying amounts of iron-staining, and the septate whorls usually consist of recrystallized calcite. The very large specimen of *Sphenodiscus* is somewhat different, for there is no recrystallized calcite and no iron-staining, and it might have come from a different (? higher) bed.

This *Sphenodiscus* undoubtedly indicates a Maastrichtian date, and probably Upper Maastrichtian. In Madagascar *Sphenodiscus* is known in one area, and occurs in the Upper Maastrichtian above beds with good Lower Maastrichtian ammonites (Besairie & Collignon 1960: 74, 79). In Europe the main *Sphenodiscus* fauna occurs in the Upper Maastrichtian, but one species, *S. ubaghsi* Grossouvre, also occurs in the upper half of the Lower Maastrichtian according to the zonal distribution table of Jeletzky (1951: 18–19). The occurrences of *Sphenodiscus* in the Middle East and India are not accurately dateable against other ammonites within the Maastrichtian. In North America the best stratigraphical sequence of species of *Sphenodiscus* is known in northern Mexico (Böse & Cavins 1927). The five zones in the Maastrichtian are based on *Coahuilites* and *Sphenodiscus*, and if the base of this succession corresponds to the base of the Maastrichtian, then at least the zone of *Sphenodiscus* *lenticularis* (the second zone from the bottom) would come in the Lower Maastrichtian. This is a large lenticular species with a highly complicated suture-line. The zones in Mexico and in the Gulf Coast of the United States have been discussed by Young (1960), but the question as to where the lower boundary of the Maastrichtian should be placed is not yet resolved. The other rich faunas of *Sphenodiscus* in the United States described and figured by Hyatt (1903) and by more recent workers (e.g. Reeside 1962: 136) are all Maastrichtian and some are Upper Maastrichtian, but the majority cannot be dated more accurately. The Angolan *Sphenodiscus*, therefore, probably indicates Upper Maastrichtian, but it could be as low as the upper half of the Lower Maastrichtian.

The remainder of the Barra do Dande ammonite fauna belongs to either the Polyplocum Zone at the top of the Upper Campanian or to the lower half of the Neubergicus Zone at the base of the Lower Maastrichtian, and a decision as to which zone it belongs to does not seem possible in the present state of knowledge of ammonites from these zones. The most obvious correlation is with the ammonite fauna of the Nacatoch Sand of Texas described by Stephenson (1941) which contains two of the same species of *Nostoceras*, several *Didymoceras* and *Solenoceras*, and occurs below the horizons with *Sphenodiscus* in the Kemp Clay. Young (1960: 252, 256) is undecided as to whether the Nacatoch Sand is top Campanian or basal Maastrichtian, but on the whole favours the latter. The presence of *Manambolites* in the Angolan fauna appears to favour a top Campanian age, for no species of this genus can be proved to be Lower Maastrichtian (see above p. 395). It is tempting to make a comparison with "*Manambolites*" *ricensis* Young (1963: 127) which can be proved to come from the top of the Campanian in Texas, but Young's species is so atypical of the genus as regards its suture-line, that it ought to be ignored for correlation purposes. The other Barra do Dande ammonites are useless for correlation; species of *Neophylloceras* are relatively long ranging, and *Polyptychoceras pseudogaultianum*, the only species common to both the Egito and Barra do Dande faunas, is said to range throughout the Santonian and Campanian in Japan. The evidence tends to favour the placing of all the Barra do Dande ammonites, except *Sphenodiscus*, in the Polyplocum Zone, Upper Campanian, rather than the Lower Maastrichtian, but the exact range of the various species of *Didymoceras* and *Nostoceras* has yet to be worked out.

The position of the Campian-Maastrichtian boundary adopted here is between the *Bostrychoceras polyplocum* and *Pachydiscus neubergicus* Zones. This position, rather than at the base of the Polyplocum Zone, is more likely to be adopted by a majority of ammonite and micro-palaeontologists. The succession of ammonites and zones in the European Campanian and Maastrichtian has been discussed at length by Jeletzky (1951; 1958) who included the Polyplocum Zone in the Campanian on historical grounds. The lower position of the boundary adopted by Haug (1910), Spath (1953) and other workers is less satisfactory. Reiss (1962) favours the higher position of the boundary as used by Jeletzky, and has used it in establishing the Polyplocum Zone age of the phosphate deposits in Israel. Finally Young (1960; 1963: 19–20, 64) accepts this higher position for the boundary and has applied it to his descriptions of the succession in the Gulf Coast of the United States.

(e) The Carimba fauna

The six ammonites from Carimba consist of the four specimens of *Baculites subanceps*, the single specimen of *Didymoceras* cf. *californicum* described above, and one fragment (C. 52728) of a very large indeterminable nostoceratid. The third fragment of a helically coiled ammonite listed by Spath (1951: 11) as possibly "*Didymoceras hornbyense* (Whiteaves) Haughton" is missing from the collection. These ammonites came from the Teba Formation, presumably from the upper part which is said to be rich in macrofossils (Mouta 1956: 43), and from which Haughton (1925: 264) obtained his fine fauna of *Nostoceras*, *Didymoceras*, *Solenoceras*, *Baculites*, *Menuites* and *Libycoceras*, and Haas (1943) his further examples of *Nostoceras*, *Solenoceras* and *Axonoceras*.

The presence of *Libycoceras* is sufficient to establish the Upper Campanian age of at least part of the Teba Formation, for all accurately dated occurrences of this genus are in the Polyplocum Zone, Upper Campanian (Reiss 1962: 7–12). Another subspecies of the Angolan form *Baculites subanceps subanceps* occurs in the Upper Campanian of California (Matsumoto 1959*a*: 130) and Japan (Matsumoto & Obata 1963: 59) (see p. 370 above), and the two are thought to be contemporaneous. Of the other Teba Formation ammonites, *Menuites* is relatively long-ranging (? Santonian–Lower Maastrichtian) and the heteromorphs could be either Upper Campanian or basal Lower Maastrichtian in age.

(f) The Benguela and San Nicolau faunas.

Nothing can be added to the discussions and details of these faunas given by Spath (1951: 6, 9). The Benguela fauna consists of 16 crushed specimens that are not accurately determinable and not worth describing. The San Nicolau fauna consists of two specimens of the nautiloid listed by Spath and one indeterminate *Baculites*.

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